# DISTRIBUTION AND HABITAT USE OF SELECTED SMALL AND LARGE MAMMAL SPECIES IN RELATION TO DIFFERENT LAND USE

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**DISSERTATION**

Zur Erlangung des akademischen Grades
doctor rerum naturalium (Dr. rer. nat.)

vorgelegt dem Rat der Biologisch-Pharmazeutischen Fakultät
der Friedrich-Schiller-Universität Jena

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geboren am 18. Dezember 1980 in Pößneck

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JENA, JULI 2010

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11. FEBRUAR 2011

# General Introduction

## Land use and loss of biodiversity

Human activity is unrivalled by any other one factor in its vast and continual effects on a large number of ecosystems in almost every region of the earth. For example, several thousand years ago Europe was covered by pristine natural forests and was characterized by low land use. The tremendous increase in human population size and in rising industrialisation over the past few hundred years have resulted in a radical increase in land use intensity, which have drastically shaped landscapes. As an ongoing process, these European landscapes suffered from deforestation, and forest fragmentation from spreading agricultural use (Forman and Godron 1986). In addition to habitat fragmentation, the intensification of land use caused increasing homogenisation of the remaining landscape patches (Schulte et al. 2007, Vellend et al. 2007), which resulted in an overall loss of biodiversity.

Over the past decades, biodiversity loss due to intensified land use as well as increased management of forests and open land habitats has been increasingly the focus of attention by nature conversationalists and scientists. High levels of biodiversity are important to fulfil the basic needs of humanity as a whole (Diaz et al. 2006). The characterisation and identification of different levels of biodiversity is important for quantifying its importance. Low biodiversity ecosystems can be recognised by a low number of species in a certain habitat, as well as by their instability and high susceptibility to damage caused by a variety of human and natural disturbance (Worm and Duffy 2003). The number of species, their individual properties, and their interactions among themselves and with their environment contribute substantially to the functioning and stability of an ecosystem (Loreau et al. 2001). Increased biodiversity affects ecosystem stability and persistence, and more importantly, depending on the communities and habitats investigated, has positive effects on ecosystem processes (Balvanera et al. 2006). Biodiversity additionally influences the provision of ecosystem services by changing the magnitude and temporal continuity by which energy and materials circulate through ecosystems. Accordingly, the direct effects of biodiversity loss on ecosystem processes and services can be very dramatic (Diaz et al. 2006).

On account of different needs and increasing demands for forestry and agricultural products, land use strategies and management practise are changing in a large number of forest and open land habitats. In Central European forests, monocultures of coniferous trees such as spruce or pine represent large areas, and forest management strategy involves clear cutting and replanting of trees. In Germany, spruce, pine, and other coniferous forest stands represent as much as 60% of the total forest area, while beech and other deciduous forest stands represent the

remaining 40% (www.wald-online.de). The dominance of coniferous forests in Germany has primarily resulted from the intense reforestation after the Second World War, and the high need for fast growing and easy manageable forest stands for timber production. The goal of modern silvicultural practise, however, is to transform monocultures of coniferous trees into more natural beech or mixed deciduous forest stands (MLUR 2004). For instance, ecological forest management avoids clear cutting, concentrates on harvesting single trees to raise productivity and natural tree regeneration, and attempts to maintain as well as pioneer rare tree species for natural regeneration (www.wald-und-holz.nrw.de). If feasible, the level of management of deciduous forests is maintained as low as possible to comply with the goals of nature conservation (see the National Park Hainich in Thuringia).

In grassland habitats, biodiversity is threatened by overgrazing due to enlarged livestock density, over-fertilisation, and the destruction of shelterbelts and hedges. In Germany, federal state governments initialized various programs to provide subsidies for agricultural companies (e.g. KULAP 2007, www.thueringen.de/thueringenagrar). Financial support has been provided for management strategies that reduce livestock density, use alternative grazing patterns (sheep grazing vs. frequent mechanical mowing), reduce the amount of fertiliser, and/or maintain shelterbelts and succession stripes. The main goal of modern grassland management is to support species rich grassland habitats with moderate management intensity to ensure a sustainable productivity.

Despite these initiatives to protect landscapes and biodiversity, it is not fully understood if, and to what extent, these changes in management type and intensity affect the biodiversity and ecosystem functioning of communities in the respective habitats. A various number of studies (Foley et al. 2005) have reported a correlation between the loss of biodiversity in single habitats with increased land use, but they have often neglected to examine the direct link between patterns of species occurrence with biotic and abiotic factors across different taxa and trophic levels. Many previous studies were conducted over a short time period, and observations were not gathered at the same study sites. There is a need for research that simultaneously investigates the complex interactions between broad spectrums of different species groups, abiotic factors, and various numbers of different management strategies in forest and grassland habitats. Additionally, a large spatial and temporal scale is necessary to uncover the long-term effects that may vary between different regions and landscapes. Such an approach would not only allow for the observation of patterns of biodiversity loss, but for uncovering the underlying mechanisms that may alter ecosystem processes and services.

## LTER-D and the Biodiversity Exploratories

The LTER initiative (**L**ong-**T**erm-**E**cological-**R**esearch), originally established in the U.S.A. (including Puerto Rico and Antarctica), consists of 26 study sites of diverse ecosystems for the study of ecological processes that extend over vast temporal and spatial scales. The LTER-D network (www.lter-d.ufz.de) aims at consolidate different study sites and research groups in Germany and is closely linked to the international LTER network. Beyond the duration of solitary projects lasting between two to five years, one of the main goals of the Network is to collect, save, and provide diverse datasets for other scientists. Thus, LTER-D aims to provide basic knowledge to contribute to the evaluation of management strategies and to discover possible scenarios to predict changing biodiversity and their effects on ecosystems.

As a member of LTER-D, the project of the Biodiversity Exploratories (Exploratories for large-scale and long-term functional biodiversity research (www.biodiversity-exploratories.de) was founded in 2006 and aims to understand the relationship between the diversity of different taxa across different trophic levels. More specifically, the effects of land use and different management types on biodiversity, as well as the effects of changing biodiversity on ecosystem processes are the foci of the investigations. In this framework of an initiative to advance biodiversity research in Germany, and in contrast to mainly descriptive observations in the past, three large scale and long term research Biodiversity Exploratories have been established (Schorfheide-Chorin, Hainich-Dün, and Schwäbische Alb). In each Exploratory, 100 experimental plots (hereafter termed “EP”) were selected out of a larger number of initial grid plots (approximately 1000) for further research purposes. Half of the EPs are located in forest (50 EPs) and the other in grassland habitats (50 EPs) and represent the most common habitat types of the region. Across each subset of EPs in forest and grassland habitats, different management types and land use classes have been identified, ranging from protected near-natural study sites to intensively managed ecosystems. Thus, this demonstrates that in terms of biodiversity change, it is possible to use a broad spectrum of different management intensities for analyses.

The Exploratory Schorfheide-Chorin is located within a Biosphere reserve 60 km north East of Berlin (N 53° 0`, E 13° 60`) in the federal state of Brandenburg and is representative for the glacially formed lowlands of North East Germany. With a yearly precipitation of 550-580 mm, this area is one of the driest in Germany. The huge number of lakes, bogs, fens, and mires is typical for this area. The soils are characterized by glacial sediments, mostly loose sandy and peaty soils or podsols, with high soil thickness. In the forest, podsolised brown earth and podsols dominate, whereas grassland is typically found on bog soils. Forest EPs include forest

stands of pine (polewood, young, and old timber), pine beech mix (old timber), oak (old timber), beech (thicket, old timber), as well as unmanaged beech stands. Grassland plots include meadows, pastures, and mown pastures, which occur fertilized or non-fertilized, and are mown 1 to 4 times. On pastures cows and horses were grazing.

The Exploratory Hainich-Dün is located in the federal state of Thuringia close to the border to Hessen. It consists of the Hainich forest region in the south, which is one of the largest coherent deciduous forest areas in Germany (16.000 ha), the Dün forest area in the north, and surrounding grasslands around the town Mühlhausen (N 51° 13´, E 10° 28`). The Hainich National Park, established in 1997, is located at the southern edge of this area. Similar to Schorfheide-Chorin, the Hainich-Dün soils are limestone-rich (upper shell-limestone) with higher soil thickness. The dominating soil types are characterized by lessivé and pseudogley, with brown earth frequently present. Forest EPs in Hainich-Dün contain age class forests of spruce and deciduous stands dominated by beech with different usage characters: age classes (thicket, young, and old timber), continuous cover forests, and unmanaged stands. Grassland plots include meadows, pastures, and mown pastures, which occur fertilized or non-fertilized, and are mown 1 to 4 times. On pastures sheep, cows and horses were grazing.

The Exploratory Schwäbische Alb is located in the federal state of Baden-Württemberg in south western Germany and ranges around the town Münsingen, 50 km west of Ulm (N 48° 24` E 9° 29`). This area is characterized by a high altitude (as much as 850 m asl.), is comprised of calcareous bedrock, and is representative of a wide range of calcareous mountain areas. The soils are characterized by limestone and dolomite. Compared to the other Biodiversity Exploratories, soil thickness is considerably reduced in the Schwäbische Alb. The area consists of a mosaic of forest and grassland, mainly dominated by the latter and due to a long tradition of sheep herding. Forest EPs in the Schwäbische Alb include spruce (young and old timber), beech mix (thicket, old timber, < 70% beech), pure beech (thicket, young and old timber), and managed continuous cover forests of beech. Grassland plots include meadows, pastures, and mown pastures, which occur fertilized or non-fertilized, and are mown 1 to 4 times. On pastures sheep, cows and horses were grazing.

## Study organisms and main questions

Within the Biodiversity Exploratories a large number of different taxa are investigated, including vertebrates, invertebrates, plants, fungi, and various microorganisms. In this study, I present field research and analyses on selected species of small- and large-sized mammals (excluding bats). Mammal species have complex requirements with respect to their habitat as they depend on the availability of food, shelter, mating partners, and species-specific ecotones

with special abiotic attributes. Mammals are therefore ideal for investigating animal-habitat interactions because the attributes required for living are likely to depend on the habitat itself. Habitat changes due to different land use or management strategy should therefore be detectable in patterns of mammal species occurrence. Specifically, small mammals such as rodents and shrews, are widely distributed and play a major role in forest as well as in grassland ecosystems as they are a main food resource for mammalian (Korpimäki and Krebs 1996) and avian predators (Hörnfeldt et al. 1990). Moreover, they consume plants, lichens (Olofsson et al. 2004), fungi (Johnson 1996), and invertebrates (Gunther et al. 1983), and act as spore dispersers for hypogeous mycorrhizal fungi (Maser et al. 1978). Uncontrolled outbreaks of small mammal populations were reported to have negative effects on forest (Hansson and Zejda 1977) as well as on grassland habitats in Scandinavia (Myllymäki 1977). Large mammals and large herbivores in particular, affect the landscape, most importantly, by feeding on vegetation such as trees, herbs, and grasses. Thus, they are causing damage primarily by their activities of browsing, fraying, and bark stripping (Gill 1992a). It has been proposed that population densities of large herbivores rising above the carrying capacity of an environment may alter plant communities (Mysterud 2006), and thus may have a negative effect on biodiversity and ecosystem functioning (Trdan and Vidrih 2008).

In the present work I investigated the relationship between individual small and large mammal communities with different land use and management types in the Biodiversity Exploratories described above. I applied various species-specific monitoring methods, including live trapping, radio tracking, spotlight counting, and faecal pellet group counting, in order to answer the following questions:

- How do different land use types in forests and grasslands affect small mammal abundance and species richness derived by live trapping?
- What is the fine-scaled habitat use of the most abundant small mammal species in the forest, as derived by radio tracking, and is this affected by land use or habitat change?
- Does spotlight counting reliably reflect large mammal abundance and habitat use?
- How do different land use types in forests affect large ungulate abundance and habitat use, as derived by faecal pellet group counting?

Based on the existing literature (Tews et al. 2004), I hypothesize that small mammal species richness, abundance, and habitat use will be positively affected by management practice favouring high habitat structure. I further hypothesize that large mammal abundance and habitat use will additionally be positively affected by moderate management practice, because increased habitat structure is expected to provide higher food availability (Battles et al. 2001).

## Manuscript overview and author contribution

Large scale monitoring of small mammals in relation to different land use types and habitat structure

*E. Heinze, S. Boch, M. Fischer, J. Müller, D. Prati, S. Socher, E. K. V. Kalko, S. Halle*

In this study we present a large scale monitoring program of small mammals in the Biodiversity Exploratories using live trapping to investigate the link between small mammal abundance, species diversity, and habitat parameters in forest and grassland ecosystems. In the years of 2008 and 2009 species richness and overall abundance of small mammals in forest and grassland habitats increased with higher habitat heterogeneity.

I planed and organised the field work for small mammal live trapping in all Exploratories. Personally I did 33% of the field work myself, analysed the data, and wrote the manuscript. The working group of Prof. Markus Fischer (including Boch, Müller, Prati, and Socher) provided data of botanical surveys. Supervision and manuscript review was done by Prof. Elisabeth Kalko and Prof. Stefan Halle.

**Manuscript status:** in preparation for "Biological Conservation"

Fine scaled habitat use of *Myodes glareolus* and *Apodemus flavicollis* in relation to different land use and habitat structure

*E. Heinze, S. Rienow, S. Halle*

This manuscript investigates the fine scaled habitat use of the two most abundant small mammal species *Myodes glareolus* and *Apodemus flavicollis* in relation to forest management in the Biodiversity Exploratory Hainich-Dün. We found no differences in home range size or activity across different management types for both species. On average, deadwood structure was more used by both species than dense vegetation, but *M. glareolus* showed stronger relation to deadwood than *A. flavicollis*. We presume that reduced deadwood disposal due to changing management practice may disfavour small mammal abundance and habitat use.

I planed and organised the field work for small mammal radio tracking, did 50% of the field work and 40% of the data analyses, and wrote the manuscript. Sandra Rienow did 50% of the field work and 60% of the data analyses. Supervision and manuscript review was done by Prof. Stefan Halle.

**Manuscript status:** in preparation for "Journal of Applied Ecology"

Large scale monitoring and habitat use of large mammals using spotlight counting

*E. Heinze, S. Halle*

In this study we present a large scale monitoring program of large mammal in the Biodiversity Exploratories using spotlight counting to investigate species diversity, estimates of relative animal abundance, and habitat use of selected species. Density estimates were highest for roe deer, whereas habitat use of roe deer and fallow deer seemed to be segregated. However, we stress that data of spotlight counting are not necessarily suitable for being analysed in terms of habitat use of single species, because data were collected over a short period of time.

I planed, organised, and conducted the field work of spotlight counting in all three Exploratories. I analysed the data and wrote the manuscript. Supervision and manuscript review was done by Prof. Stefan Halle.

**Manuscript status:** in preparation for: "Wildlife Society Bulletin"

Habitat use of large ungulates in North East Germany in relation to forest management

*E. Heinze, S. Boch, M. Fischer, D. Hessenmöller, B. Klenk, J. Müller, D. Prati, E.D. Schulze, C. Seele, S. Socher, S. Halle*

We surveyed large ungulates in the Biodiversity Exploratory Schorfheide-Chorin using faecal pellet group counts to explore the link between ungulate abundance, habitat use, and browsing damage on trees. Habitat use of roe deer and fallow deer derived by counting faecal pellet groups revealed preference to mature pine forests with high cover of edible plants, and avoidance to deciduous forests. Browsing was higher in deciduous trees, but solely beech saplings suffered less damage than other deciduous trees at low roe deer density. Because of being a concentrate selector, we suppose roe deer to affect tree diversity by selectively feeding on species containing high quality ingredients.

I planed, organised, and conducted field work of pellet group counts, analysed the data, and wrote the manuscript. Bernd Klenk helped with field work (50%). The working group of Prof. Markus Fischer (including Boch, Müller, Prati, and Socher) provided data of botanical surveys. The working group of Prof. Schulze (including Hessenmöller and Seele) provided data of browsing damage. Supervision was done by Prof. Stefan Halle, whereas all authors reviewed the manuscript.

**Manuscript status:** published with minor changes in "Forest Ecology and Management"

# LARGE SCALE MONITORING OF SMALL MAMMALS IN RELATION TO DIFFERENT LAND USE TYPES AND HABITAT STRUCTURE

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## Abstract

Non-flying, small mammals play crucial roles in many ecosystems because they are abundant and constitute important members of food webs. Land use has a major impact on habitat structure and thus is likely to influence the distribution of small mammals as well. In this study we present the results of a two-year, standardized large scale monitoring program of small mammals in the Biodiversity Exploratories Schorfheide-Chorin, Hainich-Dün, and Schwäbische Alb using live trapping to investigate the link between small mammal abundance and habitat parameters in forest and grassland plots differing in management regimes and intensity of use. During 7650 trapping nights we trapped 1882 animals in total. *Myodes glareolus* and *Apodemus flavicollis* were the most abundant species on forest plots. *Microtus arvalis* was most abundant on grassland plots. Total numbers of trapped animals on forest plots were moderate in 2008 (n = 1262), and dropped to half in 2009 (n = 620). The decline in 2009 may be partly explained by a mast year, where high availability of deciduous tree seeds on the forest floor may have made the traps unattractive, leading to reduced trapping success. In both monitoring years, species richness and overall abundance of small mammals in the forest was higher on plots with high habitat heterogeneity. On the forest plots, numbers of *M. glareolus* were strongly associated with overall vegetation cover, in particular presence of shrubs and deadwood. Our results support other studies where *M. glareolus* reacted similarly to differences in habitat structure compared to other *Myodes* species. At our study sites, habitat heterogeneity was often enhanced by differences in management practice. Although relative abundance of *A. flavicollis* on the forest plots was partly related to shrub cover, correlation with overall cover of the plots was not as strong as for *M. glareolus*. On grassland plots, numbers of individuals were higher on plots with increased vegetation height and, thus, structural heterogeneity. However, trapping numbers in grassland habitats were not directly related to land use characterised by fertilization and the presence or the kind of livestock. We suggest that forest and grassland management should concentrate on conserving high structural habitats if a high level of small mammal diversity is desired.

**Keywords: small mammals, live trapping, land use, habitat heterogeneity**

# 1 Introduction

In the last decades policy makers and landscape managers have focused their attention on threatened mammals and large game species. But within an ecosystem, all species contribute to biological diversity and thus, are important components of functional ecological communities (Bellows et al. 2001). We need to reconsider the importance of other species groups. As human population continues to expand, and land use gets more intensive (Meyer and Turner 1992), comprehensive management decisions are necessary if we want to maintain the remaining diversity and hence functionality in human-dominated landscapes. In Central Europe, most of the small, non-flying mammals, in particular rodents are abundant. They are widely distributed and both generalist as well as specialist species (Morris 1996). Small mammals play several important roles in forest and grassland ecosystems: (1) they are a main food resource for mammalian (Korpimäki and Krebs 1996) and avian predators (Hörnfeldt et al. 1990), (2) they are consumers of plants, lichens (Olofsson et al. 2004), fungi (Johnson 1996), and invertebrates (Gunther et al. 1983), and (3) they are dispersers of seeds and spores of a wide range of plants and hypogeous mycorrhizal fungi that they defecate on the floor, ensuring the survival and health of several mycorrhizal-related and other plants (Maser et al. 1978). Because of their rather ubiquitous distribution, small mammals are likely affected by any kind of structural and temporal disturbance in their habitat, mainly caused by anthropogenic influence. Therefore, changes in land use are very likely to have effects on small mammals (Fitzgibbon 1997) and their associated functions in the ecosystem.

Modern silvicultural practice has lead and will be leading to considerable changes in forest habitats over the next decades. Today, pine (*Pinus sylvestris*) and Norway spruce (Picea abies) monocultures dominate and represent a large proportion of the forested area of Germany and Central Europe (Parviainen et al. 2007). The long-term goal of modern forest management is to transform these monocultures into more natural beech or mixed deciduous forests (Parviainen et al. 2007). Indeed, the ongoing forest transformation is likely to have an impact on the habitats suitable for many forest species. In grassland habitats, small mammals are threatened by overgrazing due to increased livestock density (Rosenstock 1996) and destruction of shelterbelts and hedges. In Germany financial support has been provided for management strategies that reduce livestock density, use alternative grazing patterns (sheep grazing, e.g. KULAP 2007, www.thueringen.de/thueringenagrar), and maintain shelterbelts and succession stripes. The main goal of modern grassland management is to support species rich grassland habitats with moderate management intensity to ensure a sustainable productivity and biodiversity. However, the reactions of small mammals to structural changes in habitat attributes and different

management are not completely understood. As a change in management practise may result in differences in habitat structure such as the amount of vegetation cover, small mammal abundance and diversity may be affected as well. Hence, we compare habitat types characterized by different management schemes in terms of species diversity and abundance of small mammals to evaluate the importance of near natural and managed landscapes for this species group.

The "habitat heterogeneity hypothesis" assumes that structurally complex habitats may support a higher number of species because of more niches and ways of using the available resources (Bazzaz 1975). In most habitats the physical structure of the environment is determined by the plant community, which in return has a strong effect on the distribution of animal species. Furthermore, forest management has an influence on the amount of woody debris and the structure of shrub and tree layer (McCarthy and Bailey 1994). Hence, we assume that habitat availability determines the abundance of species of small mammals at least on a local scale. Small mammal species richness was reported to be higher in structural complex forests (Sullivan and Sullivan 2001), and species composition and abundance is positively influenced by forest management and increased habitat heterogeneity (Tews et al. 2004). Even forest clear-cutting had positive effects of small mammal abundance due to increased herbaceous understory on recently cut sites (Kirkland 1990). In grassland habitats the general composition of small mammal communities was also suggested to be primarily determined by structural attributes of the habitat (Grant et al. 1982). Small mammal species richness and abundance was reported to be higher on ungrazed sites, because increased grass cover and aboveground biomass provided more food and cover (Rosenstock 1996). Livestock presence may therefore have a direct impact on small mammals not only by grazing, but also by trampling and compacting soil (Heske and Campbell 1991). It was even suggested that different types of grazing between sheep and cattle were likely to be recognized in the abundance of grassland small mammals (Evans et al. 2006). Thus, the effects of land use and different management on small mammals may vary between forest and grassland habitats, and have to be studied on a large scale.

Most former studies dealing with small mammals in relation to land use were often restricted to small scale study areas, and did not take a broad spectrum of differentially used habitats into account. The effect of land use was mainly investigated by comparing highly managed study sites (e.g. clear-cuts, intensively grazed grasslands) with undisturbed ones, lacking observations of intermediate management intensity. In our study we investigated a broad spectrum of structural variables which are supposed to affect small mammal distribution, and

may vary among different types of forest and grassland management. More specifically, we analysed the effect of forest and grassland management types on small mammal distribution and community structure. We address the following questions: (1) which habitat variables revealed by ground surveys predict species richness of small mammal and their abundance, (2) how these variables are related to species richness and abundance of small mammals, and (3) are there any keystone structures that predict habitat use of small mammals. Based on the existing literature (Rosenstock 1996, Tews et al. 2004) we hypothesize that small mammal species richness and abundance in forests and grasslands is positively affected by high habitat structure. To our knowledge this is the first study which aims at monitoring small mammals on a large scale ranging from intensively managed grasslands to unmanaged natural forests. Our results may be valuable in predicting changes in small mammal community with changing management practice in forest and grassland habitats. Because of a high importance of small mammals especially in forest ecosystems, our results may not only be relevant for small mammal diversity and conservation, but can be interpreted in terms of ecosystem functions such as effects on food chains and seed dispersal.

## 2 Materials and Methods

### *2.1 Study area*

Small mammal monitoring was carried out in the Biodiversity Exploratories Schorfheide-Chorin, Hainich-Dün, and Schwäbische Alb (see: www.biodiversity-exploratories.de and Fig.1). In each area 100 experimental plots (hereafter named EP) were established, with 50 EPs in the forest and 50 EPs in grassland habitats.

The Exploratory Schorfheide-Chorin is located within a Biosphere reserve 60 km north-east of Berlin (N 53° 0`, E 13° 60`) and is shaped by glacial habitat characteristics and a yearly precipitation of 550 mm. Soils are characterized by glacial sediments, mostly loose sandy and peaty soils or podsols with high soil thickness. Forest plots include pine (young, old timber), pine beech mix (old timber), oak (old timber), beech (thicket, old timber, unmanaged).

The Exploratory Hainich-Dün contains the Hainich region, the largest coherent deciduous forest area in Germany, surrounding forests (Dün), and grasslands around the town Mühlhausen (N 51° 13´, E 10° 28`). In Hainich-Dün soils are composed of limestone and loess with a large soil thickness comparable to the Schorfheide-Chorin. Forest plots in Hainich-Dün consist of age class forests of spruce and deciduous stands dominated by beech with different types of usage: age classes (thicket, young, old timber), selection forests, and unmanaged stands.

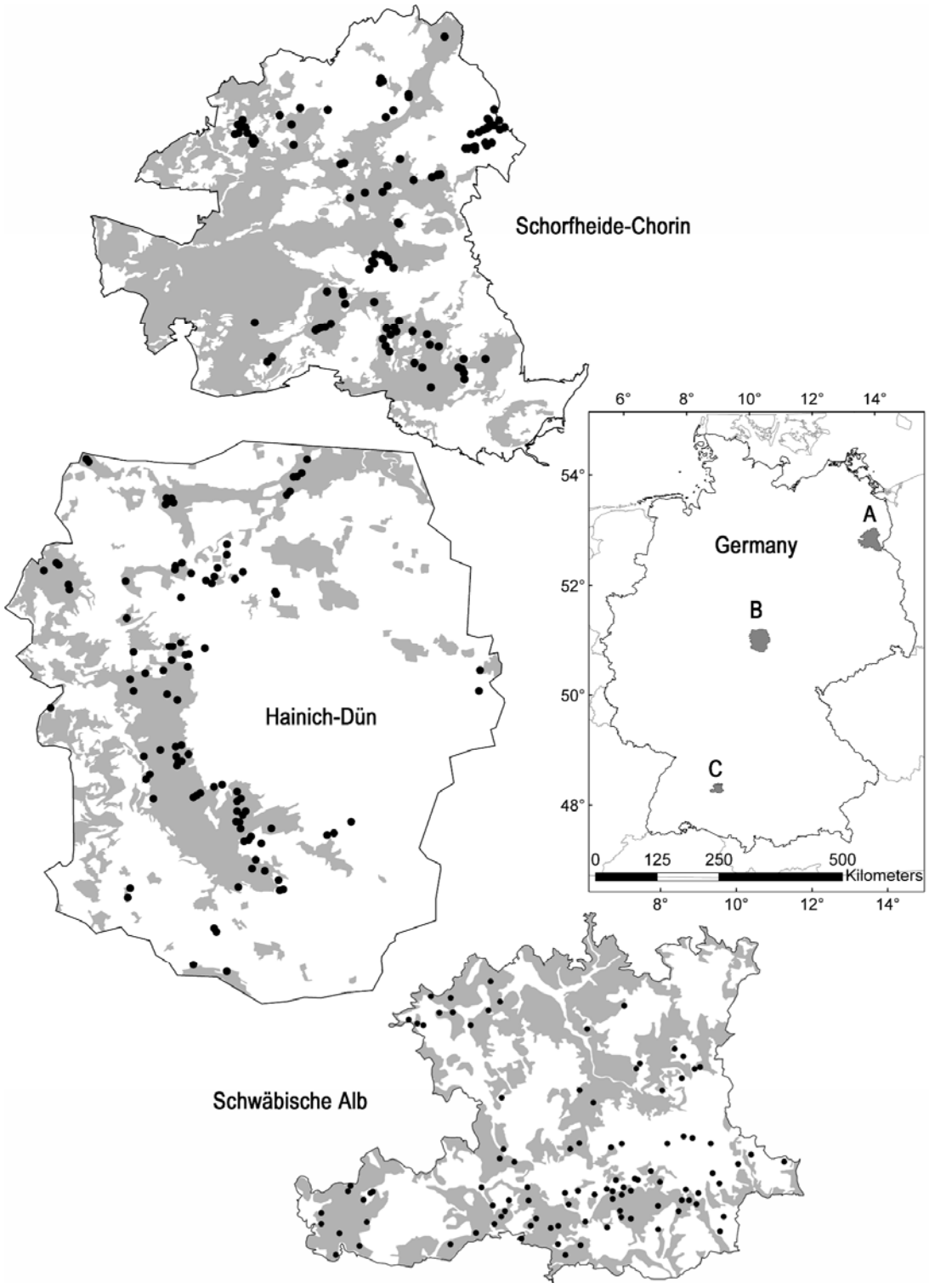


**Figure 1:** The Biodiversity Exploratories Schorfheide-Chorin (A), Hainich-Dün (B), and Schwäbische Alb (C) with experimental plots (EPs) symbolized by black dots. Forest areas highlighted in grey, white represents non-forested land including grasslands.

The area of the Exploratory Schwäbische Alb is centred around the town of Münsingen, 50 km west of Ulm (N 48° 24` E 9° 29`) and is characterized by altitudes of up to 850m asl. Soils are based on limestone and dolomite. Compared to the other Exploratories, the soil thickness is considerably lower in the Schwäbische Alb. Forest EPs in the Schwäbische Alb include spruce

(young, old timber), mixed beech forests (thicket, old timber, < 70% beech), pure beech forests (thicket, young, old timber), and selection forests of beech.

Grassland plots in all three Exploratories include meadows, pastures, and mown pastures. All three land use types occur fertilized or non-fertilized, and the amount of mowing on the meadows varied from 1 to 4 times. The mown pastures were mown once, either at the beginning or at the very end of the vegetation period. On pastures sheep, horses and cows were grazing, although sheep were missing in the Schorfheide-Chorin.

*2.2 Explanatory variables*

For analyses of the data from forest plots we recorded the forest type based on the dominant tree species (assessed by the local management teams and foresters in the Exploratories). Management reflected different types of forest land use (unmanaged or managed forests), and specific management types represented the different categories of the managed stands (selection forests with uneven-aged structure, and categories of age-class forests with even-aged structure) (Tab.1). We estimated the percentage cover of structural parameters, such as large trees (woody plants of upper canopy layer > 5m height), shrubs (all woody plants < 5 m height), herbs (recorded in summer), and deadwood. We included the Shannon diversity and evenness of shrubs and herbs into the explanatory variables as a measure of plant diversity. Data on plant cover and diversity were gathered on a fixed grid of 20 x 20 m on forest plots.

On the grassland plots, the land use types were characterized by meadows, mown pastures, and pastures. The grassland management was characterised by the frequency of mowing, the presence and kind of livestock, and the application or absence of fertilizer. Additionally, at the time of trapping we calculated the number of days after mowing and estimated the vegetation height in 10 cm classes.

*2.3 Live trapping*

We live trapped small mammals in two years during eight weeks from August to September 2008 and 2009, when their populations had reached the highest annual density (pers. comm.). 1500 “Ugglan” multiple live capture traps (“Grahnab”, Sweden) were set along fixed line transect at 10 m spacing between the traps on a total of 300 study plots (100 each per Exploratory). Traps were baited with oats, mouse pellets (Altromin), and fresh pieces of apple. We prebaited the traps and left them open for two consecutive days. Immediately, afterwards we conducted three consecutive nights of trapping, after we renewed the bait each evening before trapping. We trapped overnight, checked the traps during the morning between 7 and 10 a.m.,

and left the traps open during the day. When an animal had entered a trap we determined the species in the field according to nature field guides (Görner and Hackethal 1988). If trapped for the first time, individuals were marked with fur cutting on the back lasting more than one week (pers. comm.) to recognize recaptures. After species identification and fur cutting we released the animal on the respective plot. We used the number of first captured animals on the 300 study plots as a relative animal abundance. Due to small sample sizes and occasional low recapture rates it was not possible to apply any mark recapture indices (e.g. Jolly-Seber, Schumacher-Eschmeyer).

**Table 1**: Explanatory variables for analyses of abundance data in live trapped small mammals per experimental plot in forest and grassland habitats

| | Unit | Range |
|---|---|---|
| **Forest** | | |
| Stand type | - | beech, beech mix, oak, spruce, pine |
| Management | - | unmanaged, selection forest, age class forest |
| Age class | - | old timber, young timber, pole wood, thicket |
| Cover Trees | % | 1, ... , 99 |
| Cover Shrubs (< 5 m) | % | 0, ... , 98 |
| Cover Herbs (summer) | % | 0, ... , 95 |
| Cover Deadwood | % | 0, ... , 40 |
| Diversity/Evenness shrubs | - | |
| Diversity/Evenness herbs | - | |
| **Grassland** | | |
| Land use | - | meadow, pasture, mown pasture |
| Mowing frequency | - | no, one, two or three cuts |
| Time after mowing | days | 1, ... , 50 (in 10 day classes) |
| Vegetation (grass) height | cm | 5, ... , 80 (in 10 cm classes) |
| Fertilization | - | yes or no |
| Livestock presence | - | yes or no |
| Kind of livestock | - | cattle, horse, sheep |

*2.4 Statistical analyses*

Statistical analyses were done with SPSS 15.0 and SPLUS 6.1. Data of species richness and abundances were root transformed to obtain normality and homogeneity of variance. The Pearson correlation coefficient, ANOVA, and linear regression models (simple and stepwise multivariate) were used for analysing trapping data and explanatory variables. Differences of trapping data between the land use categories in forest and grassland habitats were analysed with ANOVA, but the land use categories were not included in the regression models.

# 3 Results

## *3.1 Comparison of trapping success*

In 2008 we captured a total of 1262 small mammals (first and recaptures) during 3720 trap nights on forest and grassland plots in all three Exploratories. Trapping success was highest in Schorfheide-Chorin with 585 captures, intermediate in Hainich-Dün with 401 captures, and lowest in the Schwäbische Alb with 276 captures (Tab.2). Overall trapping success on grassland plots (n = 199) was approximately five times lower than on forest plots (n = 1063). Trapping success differed widely between years. In 2009, 3930 trap nights yielded only 620 captures, which was about half of the trapping success of 2008. Compared to 2008 trapping success was intermediate in Schorfheide-Chorin with 192 captures, highest in Hainich-Dün with 237 captures, and similar in the Schwäbische Alb with 183 captures. More specifically, the difference of trapping numbers between the years was most distinct in Schorfheide-Chorin (Fig.2-B). Although numbers of individuals on forest plots were lower in 2009 compared to 2008, numbers of individuals on grassland plots did not reveal significant difference between years (Fig.2-A).

**Table 2**: Total trapping success of all species in the Exploratories. Trapping numbers of 2008 are followed by numbers of 2009, and summed up for each year, species, and plot type.

| | **Schorfheide-Chorin** | | **Hainich-Dün** | | **Schwäbische Alb** | | **Sum 2008** | **Sum 2009** |
|---|---|---|---|---|---|---|---|---|
| | 2008 | 2009 | 2008 | 2009 | 2008 | 2009 | | |
| **Grassland:** | | | | | | | | |
| *Apodemus agrarius* | 1 | 5 | 0 | 0 | 0 | 0 | 1 | 5 |
| *Crocidura leucodon* | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 |
| *Micromys minutus* | 4 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| *Microtus arvalis* | 114 | 107 | 47 | 84 | 3 | 1 | 164 | 192 |
| *Microtus oeconomus* | 11 | 1 | 0 | 0 | 0 | 0 | 11 | 1 |
| *Sorex araneus* | 9 | 7 | 1 | 3 | 4 | 0 | 14 | 10 |
| *Sorex minutus* | 0 | 1 | 2 | 4 | 1 | 0 | 3 | 5 |
| | | | | | Sum grassland | | **199** | **213** |
| **Forest:** | | | | | | | | |
| *Apodemus agrarius* | 1 | 5 | 0 | 1 | 0 | 0 | 1 | 6 |
| *Apodemus flavicollis* | 218 | 12 | 141 | 24 | 90 | 33 | 449 | 69 |
| *Apodemus sylvaticus* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Glis glis* | 0 | 0 | 6 | 0 | 0 | 1 | 6 | 1 |
| *Microtus agrestis* | 13 | 11 | 2 | 1 | 0 | 0 | 15 | 12 |
| *Myodes glareolus* | 193 | 18 | 192 | 99 | 163 | 143 | 548 | 260 |
| *Sorex araneus* | 20 | 24 | 7 | 11 | 15 | 0 | 42 | 35 |
| *Sorex minutus* | 1 | 1 | 1 | 10 | 0 | 5 | 2 | 16 |
| | | | | | Sum forest | | **1063** | **407** |

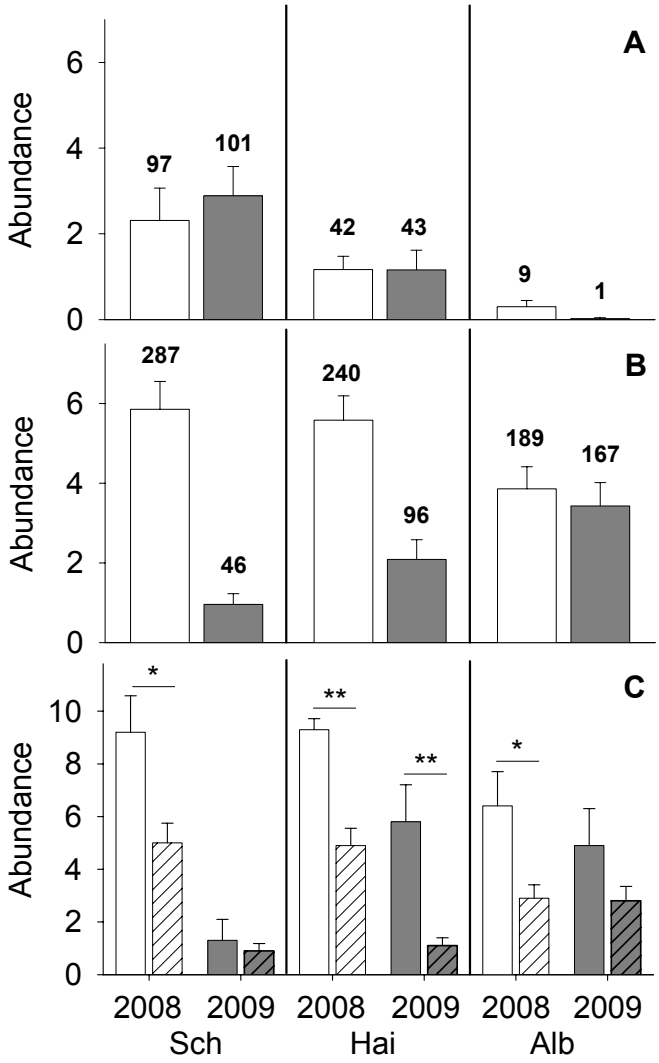


**Figure 2:** Relative abundance of small mammals (with total numbers of captures given above bars) computed as first captures per grassland (A) and forest (B) plot, in the Exploratories Schorfheide-Chorin (SCH), Hainich-Dün (HAI), and Schwäbische Alb (ALB) for 2008 (white bars) and 2009 (dark grey bars). Comparison between animal numbers in forest type thicket stage (un-hatched bars) and the other forest types, represented by unmanaged forests, selection forests, and old timber age class forests (hatched bars) presented below (C).

*3.2 Species richness on forest plots*

The species richness on forest plots increased with increasing habitat heterogeneity. On the forest plots species richness of small mammals was equal in both years for the Schorfheide-Chorin and Hainich-Dün (2008 and 2009 n = 6) and lower in the Schwäbische Alb (2008 n = 3, 2009 n = 5). In both years, the species most frequently trapped in the forest were *Myodes glareolus* (bank vole), *Apodemus flavicollis* (yellow necked mouse), followed by *Sorex araneus* (common shrew) and *Microtus agrestis* (field vole).

In both years species richness in Schorfheide-Chorin was higher in pine forests ($p < 0.05$) than in beech or mixed pine beech stands, and higher in age class forests than in unmanaged forests ($p < 0.01$). Furthermore species richness in 2008 was higher on plots with higher shrub cover ($R^2 = 0.12$*) (Fig.3).

In Hainich-Dün we found a higher species richness in age class forests than in unmanaged forest stands (2008, 2009: $p < 0.01$), resulting in higher species richness on plots with reduced tree cover ($R^2 = 0.11$*), and higher cover of deadwood ($R^2 = 0.16$**) in 2009.

In the Schwäbische Alb species richness in 2008 was significantly higher in beech and mixed beech stands than in spruce ($p < 0.01$). However, we did not find significant differences of species richness between the stand types for 2009. In 2008, species richness in thicket stages tended to be higher than in all other age classes ($p = 0.06$). Additionally, higher species richness was associated with high shrub cover ($R^2 = 0.24$**) in 2008, but not in 2009 (Fig.3).

Summarizing our results, overall variance of species richness in forests was best explained by shrub cover in 2008: $R^2 = 0.1$***, and herb cover combined with the inverse relation of tree cover in 2009: $R^2 = 0.12$**. Thus, reduced canopy cover seemed to induce the growth of herbs and shrubs, and in return the species richness of small mammals.

*3.3 Abundance of small mammals in forests*

As with species richness, relative abundance of small mammals was higher in those habitats that had high ground cover and structural heterogeneity.

In both years numbers of individuals of all species trapped were significantly higher in managed forests than in unmanaged forests of Schorfheide-Chorin ($p < 0.01$), and lowest in forests of old timber ($p < 0.05$) in 2008. *M. glareolus* showed a similar pattern in both years ($p < 0.01$). Additionally numbers of all animals (2008: $R^2 = 0.16$**, 2009: $R^2 = 0.1$*), *M. glareolus* (2008: $R^2 = 0.1$*), and *A. flavicollis* (2008: $R^2 = 0.1$*) were higher with high shrub cover (Fig.3).

In Hainich-Dün more individuals of all species were trapped in managed forests than in unmanaged forest stands (2008, 2009: $p < 0.01$). Accordingly, *M. glareolus* showed higher numbers of individuals in managed forests than in unmanaged forest stands (2008, 2009: $p < 0.01$). Explanatory variables other than forest types had no effects on patterns of small mammal abundance in 2008. In 2009 we observed higher numbers in all species including *M. glareolus* with higher cover of deadwood ($R^2 = 0.14$**), and with higher diversity of herbs as a functional group on the forest floor ($R^2 = 0.15$**). In both years the numbers of individuals in

all species was higher on plots with low tree cover. This difference, however, was statistically not significant.

In the Schwäbische Alb relative abundance of small mammals was significantly higher in deciduous than in spruce forests ($p < 0.01$), as well as in age class compared with selection forests ($p < 0.05$), and in thicket stages in contrast with the other age classes ($p < 0.05$). By comparison, numbers of *M. glareolus* in 2008 were also higher in deciduous than in spruce forests ($p < 0.05$), and in thicket stages than in age classes of young timber ($p < 0.01$). Additionally, the number of captures in all species was higher in both years on plots with high shrub cover (2008: $R^2 = 0.37$***, 2009: $R^2 = 0.2$**). Number of *M. glareolus* were also higher on plots with high shrub cover (2008: $R^2 = 0.3$***, 2009: $R^2 = 0.23$**), and on plots with low tree cover (2008: $R^2 = 0.11$*, 2009: $R^2 = 0.14$**). In 2008 animal numbers of *A. flavicollis* were more frequently trapped on plots with high shrub cover ($R^2 = 0.14$*) as in Schorfheide-Chorin.

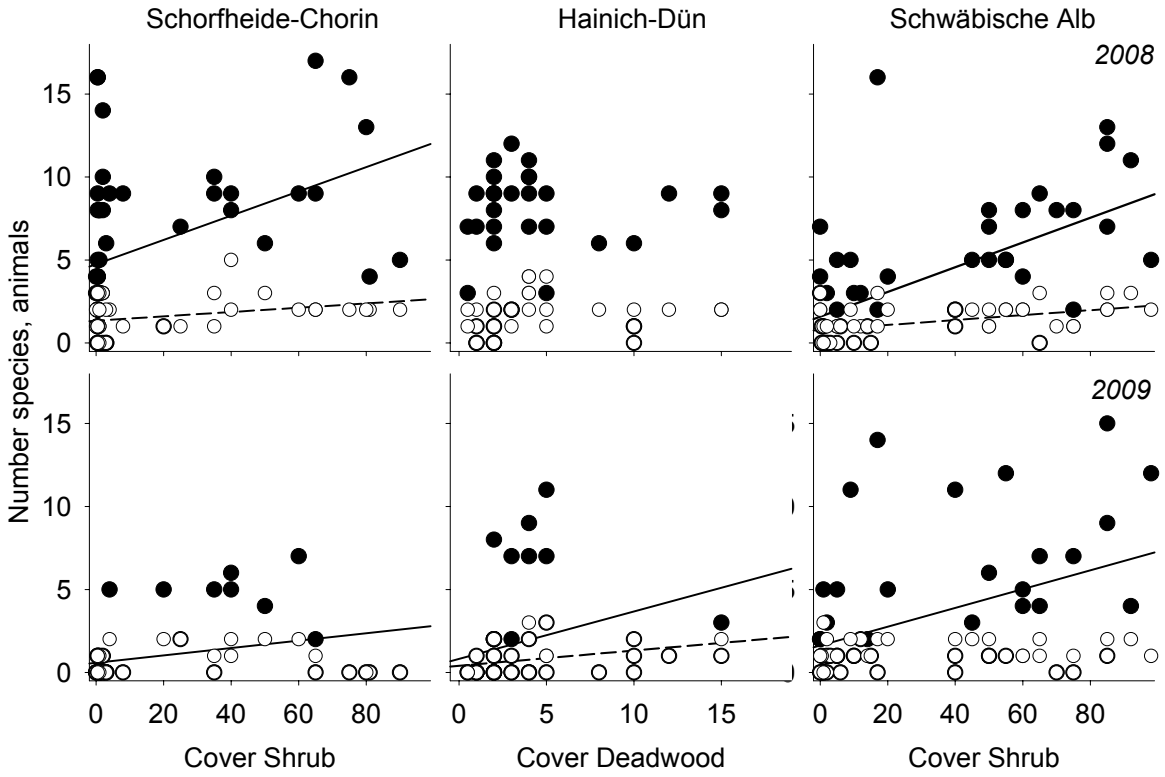


**Figure 3:** Species number (white dots) and relative animal abundance of all species (black dots) in the Exploratories Schorfheide-Chorin, Hainich-Dün, and Schwäbische Alb on forest plots for both years and the most important explanatory variable. Lines represent significant linear regression models for animal abundance (black lines) and species number (dashed lines).

Conclusively numbers of small mammals in all Exploratories were almost exclusively higher in managed forest stands, whereas thicket stages had higher numbers of individuals than the other age classes (Fig.2-C). In 2008 overall variance of abundance in all species was best

explained by the combination of shrub cover and the inverse relation of large tree cover ($R^2 = 0.16$***), when taking all Exploratories into account. Adding herb cover to this model resulted in a higher explanation coefficient for 2009 ($R^2 = 0.2$***). In all three Exploratories there was a consistent but non-significant trend of higher numbers of *Sorex araneus* in managed forests with high cover percentages of shrubs and forbs.

*3.4 Species richness on grassland plots*

In grasslands, species richness was lowest in the Schwäbische Alb (2008: n = 3; 2009: n = 1), intermediate in Hainich-Dün (2008: n = 4; 2009: n = 3), and highest in Schorfheide-Chorin (2008/09: n = 5). On grassland plots *Microtus arvalis* (common vole) was most frequently trapped. In Schorfheide-Chorin we trapped animals of *Microtus oeconomus* (root vole), *Micromys minutus* (harvest mouse), and *Apodemus agrarius* (stripped field mouse). Because of few data, we found no interaction between species richness and land use on grassland plots

*3.5 Animal abundance in grassland*

Data on grassland plots were not related to the categories of management, but seemed to be affected by plot attributes. Due to small sample sizes no statistics could be applied to the data from the Schwäbische Alb. In both years small mammals were exclusively trapped on fertilized meadows which had been mown at least three weeks ago and reached a vegetation height of 40 cm. Hence it seemed that livestock presence disfavored small mammal occurrence on grassland plots in the Schwäbische Alb.

In both years trapping numbers of small mammals tended to be higher on study plots with high vegetation height in Hainich-Dün, although not being statistically significant. However, there was no significant difference of the numbers of individuals between meadows, pastures, and mown pastures, between fertilized and un-fertilized plots, as well as between the presence/absence and the kind of livestock.

In 2008 we found higher numbers of individuals in all species with increased time since the last mowing in Schorfheide-Chorin ($R^2 = 0.31$***), and trapping numbers were highest after four to five weeks growing time. In 2008 we found, however, no significant difference of trapping numbers between meadows, pastures, and mown pastures, between fertilized and un-fertilized plots, as well as between the presence/absence and the kind of livestock. In 2009 more animals were trapped on meadows ($p < 0.01$) than on pastures or mown pastures. Similar to 2008, numbers of individuals were higher on plots with high vegetation growing time ($R^2 = 0.5$***), and vegetation height ($R^2 = 0.5$***) in 2009. Comparable to 2008, we did not

find significant differences of trapping numbers between fertilized and un-fertilized plots, as well as between the presence/absence and the kind of livestock.

# 4 Discussion

In this study we assessed how small mammal distribution is affected by different land use types in forests and grasslands. By comparing a broad spectrum of different land use types we aimed at answering the question whether changing management favors or disfavors the abundance and species richness of small mammals.

## *4.1 Species richness and abundance of the small mammal community in forests*

We found higher species richness and abundance of small mammals on forest plots with increased structural heterogeneity. Structural heterogeneity was represented by different parameters. While species number and abundance was directly correlated with shrub cover in Schorfheide-Chorin and the Schwäbische Alb, decreased large tree cover in Hainich-Dün seemed to have a stronger effect on the distribution of small mammals. However, such a reduction in canopy cover can result in higher structural heterogeneity on the forest floor from unmanaged to age class forests. Higher numbers of individuals with increased cover of deadwood in Hainich-Dün emphasize the importance of ground cover. Former studies revealed that species richness and abundance of small mammals in forests were positively influenced by shrub cover, understory vegetation, and structural heterogeneity (Ecke et al. 2002) due to cover (Moser et al. 2002), high food resources, and decreased predation risk (Simonetti 1989). Managed forests yielded higher numbers of small mammals (Suzuki and Hayes 2003), because thinning may accelerate the structural complexity by promoting spatial heterogeneity and diversity in plant communities (Carey and Wilson 2001). In our study cover of shrubs, trees, deadwood, and the diversity of herbs as a functional group affected the distribution of small mammal species and animal abundance. Understory vegetation combined with coarse woody debris may account for the variation of small mammal species in managed forests (Mengak and Guynn 2003), and should therefore be increased for conservation of biodiversity (Carey and Johnson 1995). Concerning habitat structure the preservation of microhabitat characteristics like deadwood and understory vegetation can provide suitable habitats for several species of small mammal, and would require minimal management efforts (Bellows et al. 2001).

*4.2 Abundance of Myodes glareolus in relation to forest types*

*Myodes glareolus* was the small mammal species most frequently trapped on our study plots in forests, followed by *Apodemus flavicollis* and *Sorex araneus*. The abundance of *M. glareolus* was strongly related to habitat structure such as shrub cover. This is in line with earlier studies demonstrating a positive influence of shrub cover and structural heterogeneity on the relative abundance of *M. glareolus* (Ecke et al. 2002). Also, the north American ecological equivalent to the European *M. glareolus*, *Myodes gapperi* (Kaneko et al. 1998), was most abundant in forests of different management (Swan et al. 1984).

Furthermore, *M. glareolus* was reported to favor habitats with developed undergrowth and fallen logs and branches, using these structures as burrows (Miklos and Ziak 2002). Also *M. gapperi* was numerous in managed pine stands (Sullivan et al. 2005) and more abundant on sites with high understory cover, numerous fallen logs (Nordyke and Buskirk 1991) and high above ground debris, all being suitable as refuge and nest sites (Yahner 1992). The high number of *M. gapperi* in habitats of dense woody understory and low densities of small trees was also explained by decreased predation pressure (Yahner 1982), as well as by mesic conditions in soil and litter which meet the animals' requirements for moisture while foraging (Yahner 1986). We did not find a direct relation between the abundance of *M. glareolus* and coverage of herbs as a functional group, although this was proposed to be an important habitat characteristic for this species (Mazurkiewicz 1994, Fitzgibbon 1997, Johannesen and Mauritzen 1999). However, high numbers of *M. glareolus* with decreased canopy cover may indicate an indirect relation to the understory herb layer. The richness of vascular plant species is higher in managed forests, which can be explained by the better light conditions due to the reduced tree canopy cover (Degen et al. 2005, Smith et al. 2008, von Oheimb and Härdtle 2009).

*4.3 Abundance of Apodemus flavicollis in relation to forest types*

Abundance of *Apodemus flavicollis* was not as strongly related to habitat structure as it was for *M. glareolus*. Analyses in Schorfheide-Chorin and the Schwäbische Alb revealed a positive relation of *A. flavicollis* to shrub cover, but values were not as high as for *M. glareolus*. It was reported that forest management may have a minor influence on the distribution and abundance of *A. flavicollis* (Marsh et al. 2001), but a preference to high coverage of shrubs may occur (Miklos and Ziak 2002). *Peromyscus leucopus*, the North American ecological equivalent to *Apodemus spp.* (Montgomery 1989), lives on sites with low tree density and high shrub cover. This is consistent with the arboreal behavior reported in this species (Dueser and Shugart 1978).

As habitat structure represented by shrub cover, large tree cover, and deadwood had a minor effect on animal numbers of *A. flavicollis*, other parameters should affect the distribution of this species. In former studies, mainly canopy cover, and number of seed tree species explained the abundance of *A. flavicollis*, since high level of canopy cover indicate mature woodland, leading to high tree seed crop (Marsh and Harris 2000). Contrary to our findings *A. flavicollis* was reported to be almost exclusively trapped in mature and old wood plots (Capizzi and Luiselli 1996), and differing tree seed production in mature forest stands caused variation in population densities of *P. leucopus* (McCracken et al. 1999) and *A. flavicollis* (Stenseth et al. 2002). Here, we did not find higher abundances of *A. flavicollis* in mature forests. This indicates that habitat structure was more important in determining the distribution of individuals across different forest types. However, the massive decline in animal numbers of *A. flavicollis* in 2009 may have been affected by tree seed occurrence, since tree seeds were more numerous in this year than in 2008 (pers. comm.). We suggest that low numbers of individuals in 2009 resulted from reduced trapability due to increased food supply on the forest floor. Another reason for low animal numbers in 2009 could be the absence of a seed mast in 2008 combined with a harsh winter 2008/09, which may have led to low animal densities in the following year. Weather conditions during winter on the one hand were supposedly harsh in the Schwäbische Alb due to high altitude and high snowfall. However, at low temperatures a thick layer of snow may positively affect small mammal survival due to isolation and reduced predation pressure (Hansson and Henttonen 1985). On the other hand low temperatures and little snowfall may have reduced small mammal survival in Schorfheide-Chorin, and resulted in a population decline in 2009.

### *4.4 Abundance of Sorex araneus in relation to forest types*

For *Sorex araneus* there was only a weak inverse relationship with large tree cover across the Exploratories. Non significant trends of higher shrew abundance in managed forests with high cover of herbs (Yahner 1986) can be linked to ground dwelling invertebrate diversity and abundance. High shrub cover, as well as dense layers of herbs and mosses favors the abundance of invertebrate prey species such as beetles. Increased beetle abundance correlates with high shrew predation (Churchfield 1982) and can therefore contribute to the conservation of insectivore small mammal species.

*4.5 Small mammal species richness and abundance on grassland plots*

The low trapping success on grassland plots could be the result of the rather little time that had passed since occasional mowing events, as reduced ground cover leads to decreased animal trapability. Furthermore, small mammals may be prone to evade from higher risk of avian predation if grasslands are freshly mown, and migrate into surrounding hedges or fields with existing cover. Higher numbers of individuals with higher vegetation growing time and livestock absence in the Schwäbische Alb and Schorfheide-Chorin indicate a negative relationship between small mammal abundance and grassland land use. A negative relationship between small mammal abundance and grassland exploitation has been recorded in studies focusing on the effect of grazing intensity (Evans et al. 2006). Different numbers of small mammals in grassland between the Exploratories are supposedly due to variances in soil depths and soil structure caused by different potential for burrowing. As grassland plots in Schorfheide-Chorin (sandy and peaty soils) and in Hainich-Dün (limestone soils) had larger soil thickness than in the Schwäbische Alb, this might alter the abundance of the most common grassland species *Microtus arvalis*. Optimal soil conditions in Schorfheide-Chorin in terms of soil thickness and looseness may have resulted in very high animal numbers especially of *Microtus arvalis*.

Higher species richness on grassland plots in Schorfheide-Chorin was caused by the occurrence of three small mammal species, which were not present in the other Exploratories. *Microtus oeconomus* has its southern boundary of occurrence in Schorfheide-Chorin (Görner and Hackethal 1988). *Micromys minutus* is a rare grassland species occurring in Schorfheide-Chorin, because it needs relatively undisturbed habitats to built nests in a stable vegetation layer (Görner and Hackethal 1988). *Apodemus agrarius*, as a species inhabiting undisturbed grasslands as well as bushy and forested areas, was more frequently trapped in Schorfheide-Chorin indicating that grassland plots may be more connected to small woodlots and shelterbelts in this area than in the other Exploratories. Shelter belts, woodlots, and a high spatial heterogeneity may conserve small mammal diversity in highly managed areas (Bignal and McCracken 1996). Hence, a high degree of land use caused by frequent mowing and livestock can decrease small mammal species richness and abundance in grassland habitats, and can act as a major threat if performed over large areas (Evans et al. 2006).

*Conclusion*

Increased habitat heterogeneity enhanced species richness and overall abundance of small mammals as well as the occurrence of the two most abundant forest species. Thus, in areas with

forest management, logging debris should be left on site as much as possible to increase structural heterogeneity. Increased light availability due to reduced canopy cover and management practice may increase growth of tall vegetation and shrubs leading to a high availability of food and shelter, and therefore may promote reproduction and survival of several small mammal species (Ecke et al. 2002). Nowadays, management strategies of forest sites especially deciduous forests are considerably changing. Forest managers often apply selection cutting, such that forest stands are left as natural as possible and still yield enough timber, though in a sustainable way. The current long term goals of forestry are mature forest stands of beech or mixed deciduous forests with continuous canopy cover. If the majority of deciduous forests will undergo these changes, resulting in major stands with little ground cover and low structural heterogeneity, abundance and diversity of small mammals will decrease. We suppose that reduced small mammal abundance and diversity in forest habitats due to lower management intensity will have an effect on many ecosystem processes. Mammalian and avian predators will lack an important food source, and dispersal of forest fungi and tree seeds (beech, oak) may be reduced.

In grassland habitats, land use in terms of frequent mowing and livestock grazing disfavored small mammal occurrence. However, the effect on the mammal community has to be distinguished between potential pest species such as *Microtus arvalis* which are abundant and may cause severe damage to grassland habitats when occurring in very high numbers, and rare species such as *Micromys minutus*. If high small mammal diversity in grasslands is desired, management intensity needs to be lowered and shelter belts as well as woodlots need to be considered as refuges especially during mowing.

# FINE SCALED HABITAT USE OF *MYODES GLAREOLUS* AND *APODEMUS FLAVICOLLIS* IN RELATION TO DIFFERENT LAND USE AND HABITAT STRUCTURE

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## Abstract

Habitat diversity and structural heterogeneity was reported to be very important for most small mammal species. High structural components were often caused by vegetation or coarse woody debris, providing food and protection against predators. Forest management was supposed to have an effect on the distribution of structural parameters. However, most studies investigating habitat use of small mammals relied on live trapping data, but radio tracking may be more suitable in providing fine scaled data for several species. In our study we investigated the fine scaled habitat use of the two most abundant small mammal species in Central European forests *Myodes glareolus* and *Apodemus flavicollis* in relation to forest management. We found no differences in home range size or activity across different management types for both species. However, the use of total cover including deadwood, shrubs, and large herbs was significantly higher for *M. glareolus*. *A. flavicollis* used total cover in proportion to its availability. In average, deadwood structure was more used by both species than vegetation structure, but *M. glareolus* showed stronger relation to deadwood than *A. flavicollis.* We presume species specific traits and behaviour to be the reasons for different habitat use in forest habitats. *A. flavicollis* as a rather fast moving species is not necessarily linked to high structural components, but shows increased activity during twilight with increased cover of deadwood. *M. glareolus* as a ground dwelling forest species is rather dependent on habitat structure, as 40% of all locations were taken in total cover. Although the reaction of the two species towards habitat structure and cover was not equal, especially deadwood played a major role in providing shelter. We presume that reduced deadwood disposal due to changing management practice may disfavour small mammal abundance and habitat use. Therefore, management strategies leading to enhanced deadwood storage on the forest floor should be applied, if the preservation of suitable microhabitats for small mammal species is desired.

**Keywords: small mammals, habitat use, radio tracking, habitat structure**

# 1 Introduction

For most small mammal species in forest habitats habitat diversity and structural heterogeneity are very important (Sullivan and Sullivan 2001, Ecke et al. 2002, Tews et al. 2004). Structural components mostly include deadwood often called as coarse woody debris (Mengak and Guynn 2003), dense woody understory e.g. shrubs (Yahner 1982), and understory vegetation e.g. herbs (Carey and Johnson 1995). In the small mammal monitoring program of the Biodiversity Exploratories we found higher animal abundance and species richness in sites with low tree canopy cover and high habitat heterogeneity represented by shrub cover. Reduced canopy cover was likely to be caused by forest management and different logging strategies, which in return affected understory plant growth and thus habitat structure on the forest floor (Smith et al. 2008). Thus, forest management had an effect on the small mammal community and resulted in increased numbers of individuals and species richness in managed forests. Data on habitat structure derived by botanical surveys (coverage data) and remote sensing (LiDAR) yielded similar results in explaining variation of small mammal abundance, whereas LiDAR data held a better explanation by combining different structural indices such as canopy gaps and shrub density (pers. comm.). However, LiDAR data failed to explain distribution of deadwood and ground vegetation on the forest floor, as this differentiation is very hard to get out of the derived indices of three-dimensional structures.

*Myodes glareolus* (bank vole) and *Apodemus flavicollis* (yellow necked mouse) were the small mammal species most frequently trapped in the forest during the monitoring program in the Biodiversity Exploratories. Both species had increased trapping numbers in highly structured habitats, whereas *M. glareolus* was more related to shrub cover than *A. flavicollis*. Beside, the relation between animal abundance and deadwood was not consistent across the Exploratories, but was only observed for *M. glareolus* in Hainich-Dün. It remains unclear if small mammals distinguish between different structural features, and if several habitat components have a higher importance for habitat use than others.

A high number of studies dealing with habitat use of small mammals rely on live trapping data, as relative animal abundances may be correlated with different habitat characteristics between study plots. However, it was reported that patterns of habitat use derived by trapping data may be biased and should be interpreted with care (Yahner 1982). Changes in relative animal abundances across study areas of different habitat characteristics can only explain trapping success on a regional scale, but may not hold information about fine scaled habitat use on a local scale. In contrast, the method of radio tracking (Kenward 2001) allows for a detailed

observation of an animal's behaviour over a period of time by creating data on a finer location scale and time scale.

Here, we present a radio tracking survey in the Biodiversity Exploratories investigating the two most abundant small mammal species in central European forests *Myodes glareolus* and *Apodemus flavicollis*. We asked the following questions: 1. is there a difference in habitat use between *Myodes glareolus* and *Apodemus flavicollis*? 2. is there a certain preference or avoidance towards specific habitat features like deadwood, shrubs, or herbs?, and 3. Is there a difference in daily activity pattern between species or between management types in the forest? Therewith we try to uncover species specific differences in habitat use and to point out the importance of certain habitat structures, which are very hard to identify with live trapping data.

## 2 Material and Methods

### *2.1 Plot selection*

In the Biodiversity Exploratory Hainich-Dün we selected six study plots by choosing one plot with high and one with low total ground cover (deadwood, large herbs, and shrubs) for each management type of age class forests, selection forests, and unmanaged forests of beech. Two plots per management type each had a minimum distance of 100m and a maximum distance of 300m. On each plot a fixed grid of 36 "Ugglan" multiple live capture traps ("Grahnab", Sweden) was set with 10m spacing between the traps.

### *2.2 Radio tracking*

We conducted two radio tracking sessions in July and September 2008. In each session two plots of one management type were sampled at a time. Prior to radio tracking we conducted a live trapping program of one week prebaiting and three trapping nights. All 36 live traps were set with oats, mouse pellets (Altromin), and fresh apple pieces as bait. We renewed absent food the evening before trapping, trapped overnight, and left the traps open during the day. When an animal had entered a trap we took it out and determined the species and the sex.

We radio tracked individuals of *Myodes glareolus* and *Apodemus flavicollis* in order to get information about fine scaled habitat use of these two frequently trapped small mammal species in central European forests. We attached activated radio collars (BIOTRACK) with cable tie to selected individuals of *M. glareolus* and *A. flavicollis* having a minimum body weight of 20g. Radio tracking on two study plots per management type lasted 72 hours. We used Telonics receivers and Yagi antennas to locate each animal every hour within its actual activity range (homing-in). Locations were obtained by taking the live traps as fixed points and estimating the

distance from each trap to the animal location with the naked eye. If an animal was located outside the trapping grid we recorded the position with a mobile GPS unit (Garmin). Additional live trapping was conducted after each radio tracking session in order to re-trap radio tagged individuals and remove the radio collars.

### *2.3 Habitat mapping*

For a detailed habitat analysis each plot was mapped on a minimum area of 100 x 100 m or larger if necessary. We mapped deadwood either from 30 cm diameter, or branches with smaller diameters forming clusters. Shrub cover was recorded including all woody plants ranging from 1-5m height. Furthermore, cover of large herbs and grasses was estimated from a minimum height of 20 cm.

### *2.4 Statistical analyses*

Location data were analysed with ArcGIS 9.2 (ESRI) and Ranges VI. Additionally a habitat selectivity index (Jacobs index) was applied (Jacobs 1974) to analyse habitat use of radio tracked individuals. This index ranges from -1 to +1, where -1 means avoidance and +1 preference to a habitat feature. Additionally the diurnality index (Halle 1995) was computed which indicates activity during night (-1) or day (+1), by taking travelling distances between location points during day, twilight, and night into account. All data were statistically analysed using SPSS 15.0 and SPLUS 6.1. Because of non normality and variance inhomogeneity we applied Kruskal-Wallis and Mann-Whitney-U tests to compare means of radio tracking data and Jacobs indices. Linear regression models were used between data of total cover use and total cover proportions, as well as activity patterns.

## 3 Results

In total we radio tagged 45 individuals, but only radio tracking data of 36 animals were used for further analyses (21 *A. flavicollis*, and 15 *M. glareolus*), as some animals lost the radio collar or disappeared during the radio tracking sessions. Data from both radio tracking sessions were pooled because there were no differences in home range size or habitat use between July and September in both species. As with the times of the year, there was no significant difference in home range size or habitat use between different sexes within each species.

*3.1 Home ranges*

We found no significant difference in home range size, neither for *A. flavicollis* (Kernel 95%, Minimum Convex Polygons MCP 95%), nor for *M. glareolus* (Kernel 95%, MCP 95%) between different management types. The average home range size (mean ± SE) of *A. flavicollis* was 2252 ± 351 m² (Kernel 95%), and 2151 ± 367 m² (MCP 95%), and of *M. glareolus* 1997 ± 724 m² (Kernel 95%), and 1700 ± 572 m² (MCP 95%).

*3.2 Use of total cover*

The use of total cover (including deadwood, shrubs, and large herbs) within the home range area was significantly higher for *M. glareolus* (44 ± 6%), than for *A. flavicollis* (20 ± 3%) (Kernel 95% $p < 0.001$). As with the areal cover use, there was a higher total cover use at single locations for *M. glareolus* (81 ± 5%), than for *A. flavicollis* (49 ± 4%) (Kernel 95%, $p < 0.001$).

In *A. flavicollis* we found an increased proportion of location points being in total cover with increased total cover on the study plot ($R^2 = 0.29^{**}$), whereas cover of deadwood explained 36% of total variance of habitat use in a separate regression model. Hence, *A. flavicollis* had a low total cover use at low total cover and deadwood availability, and vice versa (Fig.1B).

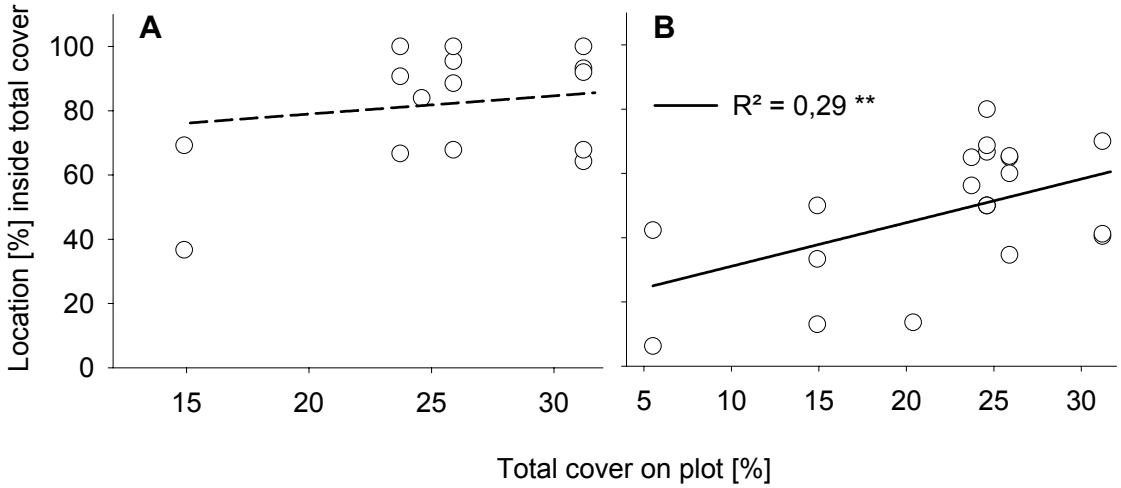


**Figure 1:** Habitat use (proportion of location points inside total cover symbolised by open circles) of *M. glareolus* (A), and *A. flavicollis* (B) depending on total cover per plot. Linear regression model is symbolised by black line for *A. flavicollis* (B). Dashed line represent non-significant regression model for *M. glareolus* (A).

In *M. glareolus* there was no interaction between location points in total cover and proportion of cover on the study plots, meaning that at least 40% of all locations of this species were taken in habitats with total cover (Fig.1A). Therefore *M. glareolus* showed no response to low total cover availability as observed in *A. flavicollis*.

*3.3 Habitat selectivity index*

Concerning habitat selection we could not find significant differences in Jacobs indices between management types for both species, meaning that habitat selection stayed constant irrespective of forest management. In average *A. flavicollis* preferred deadwood and total cover (both: 0.49 ± 0.07), while areas with no cover, shrubs, and large herbs were avoided (-0.49 ± 0.07, -0.69 ± 0.11, -0.15 ± 0.19).

As in *A. flavicollis*, *M. glareolus* on average preferred total cover and deadwood (both: 0.84 ± 0.05), and avoided areas with no cover (-0.84 ± 0.04), shrubs (-0.53 ± 0.16), and large herbs (-0.72 ± 0.16). However, *M. glareolus* showed a stronger preference than *A. flavicollis* towards total cover ($p < 0.001$) and cover of deadwood ($p < 0.001$), but had stronger avoidance towards large herbs ($p < 0.01$).

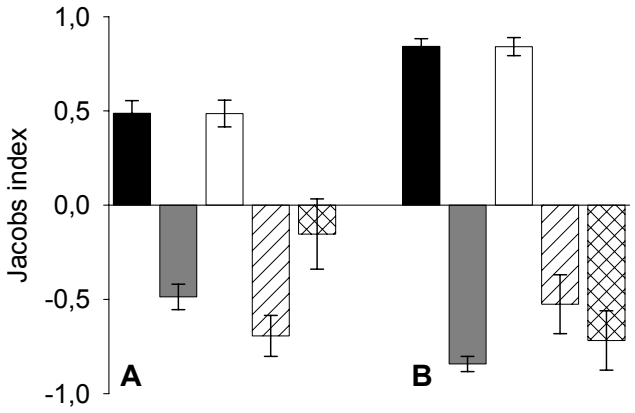


**Figure 5:** Jacobs indices of *A. flavicollis* (A) and *M. glareolus* (B) derived by radio tracking data for total cover (black bars), no cover (grey bars), deadwood (white bars), shrubs (hatched bars), and large herbs (cross hatched bars).

*3.4 Activity pattern*

The mean diurnality index derived from the radio tracking data was -0.84 ± 0.03 for *A. flavicollis*, and -0.17 ± 0.33 for *M. glareolus*. Therefore *A. flavicollis* was more active during the night. However, the diurnality index of *A. flavicollis* increased with high deadwood cover on the plots ($R^2 = 0.2$*), meaning that this species shifts its activity towards day (twilight) when more deadwood was available. In contrast, there was no interaction between diurnality index of *M. glareolus* and habitat parameters on the plots.

# 4 Discussion

Radio tracking allowed us to uncover fine scaled habitat use of the two most abundant small mammal species in central European deciduous forests, *Myodes glareolus* and *Apodemus flavicollis*. However, there was no effect of forest management on habitat use or home range size of the species. But as management strategy in forests was supposed to have an effect on canopy cover (Smith et al. 2008), amount of deadwood (Carey and Wilson 2001), and understory vegetation (Battles et al. 2001), this should have had an effect on habitat use of small mammals as well. Study plots were selected facing a trade off between plot vicinity and dissimilarity in terms of habitat parameters. An insufficient variation of habitat parameters between the study plots of different management types may be the reason for an unseen reaction of small mammal habitat use based on our categorization of different forest management.

*M. glareolus* was positively related to deadwood and total cover on the survey plots, although home ranges did not differ between the plots. *M. glareolus* used areas of total cover and deadwood almost exclusively irrespective of its proportion. In former studies the abundance of *Myodes gapperi* (the North American equivalent to *M. glareolus*) was reported to increase with high deadwood structure and log diameter (Hayes and Cross 1987). *Myodes rufocanus* was strongly related to the abundance of decayed logs as well (Bowman et al. 2000). An increased use of undergrowth by *M. glareolus* (Miklos and Ziak 2002) was explained by a high need of cover and shelter against predators (Jensen and Honess 1995). *M. glareolus* as a ground dwelling species is rather slow moving and needs good hiding availability, because it has limited flight opportunities if getting in direct contact with predators. The daily activity of *M. glareolus* was neither nocturnal nor diurnal, but rather crepuscular and did not change across different management types or total cover portions. Former studies reported that at high population densities *M. glareolus* adapted its activity pattern to avoid the bigger and stronger *A. flavicollis* (Wojcik and Wolk 1985). As *A. flavicollis* was almost exclusively active during night, *M. glareolus* might not only be active during the night, but also during the day, to reduce the proportion of direct confrontations.

The results of the present study showed a positive relation of *A. flavicollis* to total cover and deadwood, although this was not as strong as for *M. glareolus*. Our results coincide with former studies of *Peromyscus spec.* (the North American equivalent to *Apodemus spec.*), reporting higher abundance and survival of animals in areas with an increased amount of deadwood (Loeb 1999) and shelter woods (Swan et al. 1984). Higher abundance of *A. flavicollis* in dense forests covered with shrubs (Miklos and Ziak 2002) was also explained by the ability to escape predators, as it was stated for *M. glareolus*. However, *A. flavicollis* showed low total cover

usage with low total cover proportion on the study plots, which may indicate plasticity towards forest habitats with low cover and open areas on the forest floor. *A. flavicollis* as a rather fast moving species (Görner and Hackethal 1988) was therefore not as strongly connected to hiding cover as *M. glareolus* (Jensen and Honess 1995). Hence, it seemed that *A. flavicollis* has a better ability to escape if encountered by a predator. Numerous animal sightings during the radio tracking sessions especially during night support this hypothesis. Shifting its activity towards dawn with increased overall structure on the study plots, *A. flavicollis* may compensate the perceived predation risk, because deadwood and other structural components provide cover and shelter during twilight, which is a phase of high activity of mammalian predators.

Conclusively, structural heterogeneity on the plot level was very important for *M. glareolus* and *A. flavicollis*, whereas both species strongly preferred deadwood rather than large vegetation. *M. glareolus* showed stronger avoidance towards large herbs than *A. flavicollis* which may have had a better ability to escape a predator when being located in areas with tall vegetation. As a matter of fact, predators may not be hindered by tall vegetation or plants like nettles. We suggest, that deadwood represented by stumps and big log clusters provided a better hiding opportunity than herbs, because of being a stronger physical obstacle for a predator. Species specific traits seem to alter the individual usage of habitat structures, as predator avoidance acts as the main driving force in determining an animal location. As *M. glareolus* and *A. flavicollis* depended on deadwood occurrence, both species may suffer from reduced deadwood disposal due to changing forest management. Although we could not find any evidence of changes in animal behaviour between management types, even aged forests of high age and no regeneration layer (young trees) are supposed to be a suboptimal habitat for the investigated species, and small mammals as such. Hence, management strategies leading to enhanced deadwood storage on the forest floor should be applied, if the preservation of suitable microhabitats for small mammal species is desired.

# LARGE SCALE MONITORING AND HABITAT USE OF LARGE MAMMALS USING SPOTLIGHT COUNTING

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## Abstract

Monitoring of large mammals has been of particular interest to wildlife management in the last decades to uncover the link between population dynamics and environmental factors. The method of spotlight counting is often used for this monitoring purpose. In this study we present a large scale monitoring program for large mammals in the Biodiversity Exploratories using spotlight counting and distance sampling analyses to investigate species diversity, estimates of relative animal abundance, and habitat use of selected species. We found low species diversity in the Schwäbische Alb due to the absence of red deer and fallow deer. Although owing a higher species number, species diversity in Hainich-Dün was lower than in Schorfheide-Chorin. Wild boar was only counted in Schorfheide-Chorin, which we presume to be due to a high sensibility of wild boar towards the car and spotlights during counting in the other Exploratories. Density estimates were highest for roe deer. However, density estimates derived by distance sampling analyses were exclusively lower than values of basic counting indices. We suggest that imprecise density estimation during the spotlight counting resulted in errors leading to biased model fitting in the distance sampling analyses. Counting indices and harvest rates of selected species were positively related suggesting that spotlight counting data were able to reveal trends in animal populations. Habitat use of roe deer and fallow deer seemed to be segregated, although there was no direct evidence of dietary competition. Fallow deer presence was strongly correlated to either open land or pine forests, and roe deer preferred deciduous forest stands. However, we stress that data of spotlight counting are not necessarily suitable for being analysed in terms of habitat use of single species, because data were collected over a short period of time. Thus, cumulative data collection such as faecal pellet group counts seemed to have a bigger potential for gaining information about habitat use of large herbivores in forest ecosystems.

**Keywords: large mammals, spotlight counting, distance sampling, habitat use**

# 1 Introduction

Monitoring of large mammals has been of particular interest to a high number of scientists and forest managers in the past to investigate patterns of species diversity, the structure and dynamics of populations and their relation to environmental factors. Indeed, large mammals are very important, because they can hold key functions in many ecosystems. Acting as top predators, medium sized mammal species like red fox (*Vulpes vulpes*), wild cat (*Felis sylvestris*) and mustelides (e.g. *Martes spec.*) play a major role in forest food webs. E.g. predation of red fox was reported to have a stabilising impact on cycling field vole *Microtus argrestis* populations in Scotland (O'Mahony et al. 1999), and the presence of mustelides like marten and stoat were supposed to have an effect on vole reproduction and population growth (Klemola et al. 1997). The uncontrolled outbreak of small mammal populations was in return supposed to have a tremendous effect either on forest ecosystems (Hansson and Zejda 1977), or on grassland habitats (Myllymäki 1977) in Scandinavia. Large herbivores on the other hand have an effect on habitats by feeding on plants like trees, herbs, and grasses. The damage caused by present deer populations is often due to browsing, fraying, and bark stripping, although the effects may not only depend on deer density alone (Gill 1992a). By browsing on tree seedling and shrubs, deer tend to reduce stem density, limit height growth, reduce foliage density, and thus create more open understory in forest ecosystems. Especially roe deer was supposed to change tree communities through selectively feeding on several species (e.g. oak) and thus favouring the growth of others (e.g. beech) (Kullberg and Bergstrom 2001). Beside plant damage, deer species were reported to be very important for seed dispersal. As small hard seeds are more likely to survive digestion, most of the species known to be dispersed in this way include grasses and small herbs (Gill and Beardall 2001). Hence, medium sized and large mammal species are very important to be investigated in terms of species diversity and relative animal abundance over a broad spectrum of habitats.

As a direct monitoring method spotlight counting was applied as a common tool for large mammal monitoring, although the main focus was laid primarily on getting estimates of population densities than levels of species diversity. A number of medium sized species were investigated using spotlight counting such as European rabbit (*Oryctolagus cuniculus*) (Caley and Morley 2002, Poole et al. 2003), brown hare (*Lepus europaeus*) (Barnes and Tapper 1985, Verheyden 1991, Langbein et al. 1999, Heydon et al. 2000), racoon (*Procyon lotor*) (Gehrt 2002), and red fox (*Vulpes vulpes*) (Heydon et al. 2000, Ruette et al. 2003). Even wild cats (*Felis* sylvestris) were observed during spotlight counts in Belgium (Simon 2000). Additionally, a various number of deer species were monitored using spotlight counting, e.g. red deer (*Cervus*

*elaphus*) (Dzieciolowski et al. 1995, Focardi et al. 2001, Daniels 2006), fallow deer (*Dama dama*) (Focardi et al. 2001), roe deer (*Capreolus* capreolus) (Ward et al. 2004), the American mule deer (*Odocoileus hemionus*) (Austin et al. 1998), and white-tailed deer (*Odocoileus virginianus*) (Whipple et al. 1994, Naugle et al. 1996, Collier et al. 2007). Therefore, spotlight counting seemed to be a useful monitoring method which can be applied to a broad spectrum of different large mammal species ranging from red deer to medium sized carnivores (e.g. marten) or herbivores (e.g. rabbit).

Data derived by spotlight counting are indices (Anderson 2001) and they may not accurately represent real population size, because the ratio of the count to the true population is unknown (Anderson 2003). For example, previous studies (McCullough 1982, Fafarman and Deyoung 1986, Cypher 1991, Whipple et al. 1994, Focardi et al. 2001) have tried to evaluate the relative utility of spotlight counting for investigating relative deer abundances. The consensus was that observers missed a various number of individuals during spotlight surveys because of a variety of reasons. However, by replicating transects, spotlight surveys were supposed to have a high management value (Collier et al. 2007). Nevertheless, when applying the method of spotlight counting it is important not to mix the estimated values of relative animal densities with real population densities.

In particular, survey data, either derived by spotlight counting or any other direct census method, can be analysed by using the method of distance sampling (Buckland et al. 2001). During the surveys, the numbers of animals and the perpendicular distance to the animal have to be recorded. Afterwards the number of sighted animals of the selected species in the counting area is modelled as a function of the perpendicular distance of the detected animal from the transect line. Distance sampling was widely used to monitor populations of e.g. roe deer, fallow deer, and wild boar (Focardi et al. 2002), although it has been proposed that care has to be taken to satisfy the assumptions of the statistical models. Nevertheless, distance sampling provides the possibility to analyse spotlight counting data in terms of higher precision and statistical model selection, as well as creating encounter rates and mean cluster size of located animals (Buckland et al. 2001).

Although large mammal monitoring using spotlight counting was often used, most studies were restricted to areas in the temperate forests of North America and Fennoscandia. Hence, we developed a large scale monitoring program of large mammals in Germany focusing on species distribution and relative animal abundance connected to a broad range of different forest types. Therefore, the Biodiversity Exploratories as a large scale research platform were suitable for this purpose, because they focus on the diversity as well as on the relationship between diversity and

ecosystem functioning of different taxa and trophic levels. More specifically, large mammal monitoring may be valuable for other research groups by giving a basic overview of the mammal fauna in the areas of the Biodiversity Exploratories.

In this study we present a large scale monitoring program for large mammals during a one year period with emphasis on species diversity, relative animal abundance, and habitat use of the most common species in the Biodiversity Exploratories Schorfheide-Chorin, Hainich-Dün, and the Schwäbische Alb. By choosing the method of spotlight counting we tried to use a monitoring method which was applicable for a broad spectrum of different species ranging from medium sized carnivores like red fox to large herbivores such as deer. We tried to answer the following questions: 1. what levels of species diversity can be derived by spotlight counting on selected survey tracks in the Biodiversity Exploratories, 2. what estimates of relative animal abundance of selected species can be derived by spotlight counting, and how are these values related to indices of harvest rates of these species, 3. does the method of distance sampling improve the density estimates of selected species, and 4. which patterns of habitat use of selected species can be derived by spotlight counting data?

To our knowledge this is the first study which investigated large mammal distribution and habitat use applying standardised methodology and survey tracks over a wide range of Germany's forest areas.

## 2 Material and Methods

### *2.1 Study area*

We conducted spotlight counting in the Biodiversity Exploratories Schorfheide-Chorin, Hainich-Dün, and Schwäbische Alb (Fig.1) twice a year in spring and autumn from February 2007 to March 2008. We have chosen the counting tracks by taking forestry roads through various forest and open land habitats. The area selection was done in close cooperation with the landowners, forest officials, and hunters to reduce interference in certain times of the hunting season. Although each track did not cover the whole area of the Exploratory, they were supposed to represent a random sample with the most common forest and habitat types in the region. In Schorfheide-Chorin the counting track was a big loop around the village Chorin (N 52° 54′; E 13° 52′), 70 km north east of Berlin, and was divided in two 18 and 19 km long sub tracks (Fig.1). Habitat diversity across all tracks was highest in this area, containing forests with beech, oak, pine, larch, and wetlands. The survey track in Hainich-Dün was following the "*Rennstieg*" trail near the town Mühlhausen (N 51° 12′; E 10° 27′) along the Hainich forest region from north to south. The track was a 14 km section north of the National Park Hainich,

followed by a 20 km route through the National Park and adjacent forest areas in the south (Fig.1). Habitats in Hainich-Dün were dominated by deciduous forests, mainly represented by beech. In the Schwäbische Alb the counting track was located near the town Münsingen (50 km west of Ulm, N 48° 24′; E 9° 29′), and was a 20 km long L-shaped route in the west mainly dominated by coniferous forest, and a 9 km long loop in the east dominated by deciduous forest, as well as various open land habitats (farmland) (Fig.1).

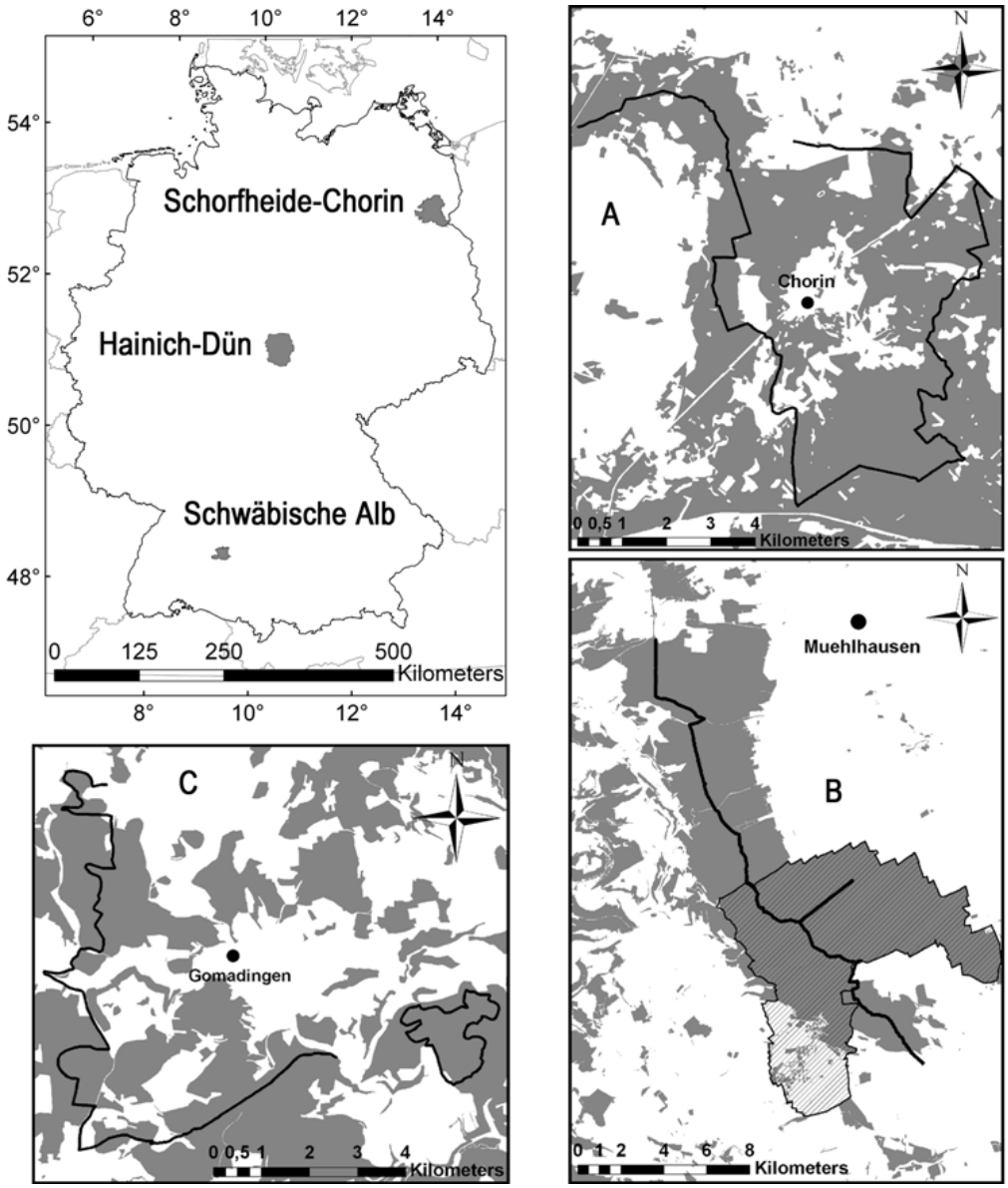


**Figure 1**: The Biodiversity Exploratories Schorfheide-Chorin (A), Hainich-Dün (B), and Schwäbische Alb (C) in Germany. The counting tracks (thick black lines) are shown in separate boxes on the right, with the National Park Hainich in the Biodiversity Exploratory Hainich-Dün (B) as hatched area.

*2.2 Spotlight counting*

During daytime we made an estimate of the visibility conditions for various habitats by driving along the tracks and recording the maximum sighting distance (minimum 5-10 m) for each habitat fragment. In open land habitats the sighting distance had a maximum estimate of 150 m (optimal visibility conditions). Beside the visibility estimate we recorded the length (meter) and the main habitat characteristics of each habitat fragment (e.g. main tree species). Each counting track had a maximum length of 40 km in total, and was split in two parts. Each part was surveyed once during one night with one replication after 48 hours, resulting in four consecutive survey nights in a week. Surveys started in complete darkness approximately at 8:00 pm and lasted up to 4 hours, depending on the track length. We have chosen starting time at 8:00 pm to avoid higher counting rates because of increased activity of the animals during twilight. Hence, twilight ended at least half an hour before we started the counting. We conducted the surveys by slowly driving (approx. 5 km/h) along forestry roads with a car and counting all observable animals in the spotlight cone on the right and left side of the car. We used two fixed spotlights on the car roof (50 Watt), and two mobile spotlights (100Watt) handled by the counting person in the car. Counting was done with two people, the driver and passenger. When recognizing an animal either by shape or by eye flashing, the species was identified as good as possible, the habitat was roughly characterised, a GPS position of the counting point was recorded, and the perpendicular distance to the sighting point was estimated in ten meter classes. If identification was not possible with the naked eye, binoculars were used. We did not distinguish between different sexes or ages of the same species. For a quick and safe data collection, sighting points were recorded in a GPS unit (Garmin) and a mobile pocket PC (Dell).

*2.3 Statistical analyses*

We calculated the potential counting area along the spotlight tracks by multiplying the length of all habitat fragments with the estimated maximum sighting distances made during the day. Furthermore, we computed counting indices of sighted animals by dividing the mean number of two counting events by the potential counting area. These values were scaled up into numbers of animals per 100 ha. The counting indices were computed for both counting sessions together and the whole counting area. Beside the counting indices data were analysed using the program DISTANCE 5.0 (Thomas et al. 2006). Furthermore, the counting indices were compared with harvest data out of the hunting lists. Data on shooting rates were collected from the local ministries of hunting in all three Exploratories, according to the areas where counting had been

done. Because we conducted spotlight counting at least until March 2008, hunting data where gathered from the winter 2007/08.

Location data of the counting events (sighting points) as well as the track data were transferred to ArcGIS 9.2 (ESRI). As projecting location data on given map files, it was possible to adjust the location points and tracks to the habitats on the maps. Location points of the counting events laying on the track were replaced into the potential sighting area by taking the perpendicular distance (m) estimated during the counting event. This was done by creating a buffer around the tracks with 15 buffer rings each having a ten meter width.

For computing species diversity we used the Shannon diversity index and Evenness to place stronger weight on the scarce species (Krebs 1999). To get information about habitat selectivity, the adjusted location data of the counting events were set against the given habitat types in the GIS. More specifically, the main habitat variables of the habitat polygons were: forest/open land, main tree species, and composition of secondary tree species. Additionally, we computed a habitat selectivity index (Jacob`s index) for selected species ranging from -1 to +1, where -1 is avoidance, 0 is no interaction, and +1 is preference to a habitat structure (Jacobs 1974).

# 3 Results

## *3.1 Habitat characteristics of survey tracks*

The distribution of habitat types differed between the counting tracks of the Exploratories due to actual differences in forest and tree composition of each region. Habitat distribution between the survey tracks of Schorfheide-Chorin and the Schwäbische Alb were similar (Fig.2), containing 20 and 23% of open land, 30 and 33% of spruce and/or pine forests, 6% (both) of conifer

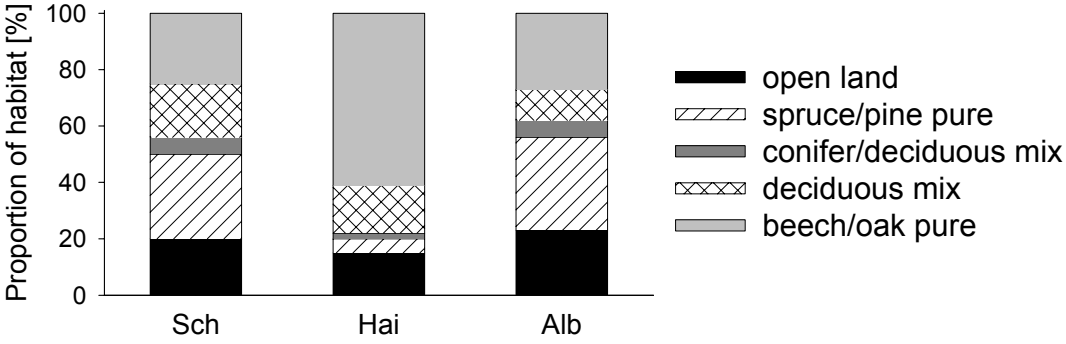


**Figure 2:** Distribution of different habitat types in the Exploratories Schorfheide-Chorin (Sch), Hainich-Dün (Hai), and Schwäbische Alb (Alb). Open land is symbolised by black bars, spruce/pine stands have hatched areas, conifer/deciduous mixed stands are represented by dark grey bars, deciduous mixed stands have cross hatched areas, and beech/oak pure stands are symbolised by light grey bars.

deciduous mixed stands, 19 and 11% of deciduous mixed forests, and 25 and 27% of pure beech and/or oak stands. The counting track of Hainich-Dün contained fewer open land (15%), spruce and/or pine forests (5%), and conifer/deciduous mixed stands (2%). However, deciduous mixed (17%) and pure beech stands (61%) had larger portions around the survey track in Hainich-Dün (Fig.2) corresponding to the high amount of beech forests in this region.

**Table 1**: Number of sighted species (S) during the spotlight counting, Shannon diversity (H), and Evenness (J) of all three Exploratories

| Species | Schorfheide-Chorin | Hainich-Dün | Schwäbische Alb |
|---|---|---|---|
| *Capreouls capreolus* | X | X | X |
| *Dama dama* | X | X | |
| *Cervus elaphus* | X | X | |
| *Sus scrofa* | X | X | |
| *Felis sylvestris* | | X | |
| *Martes spec.* | X | X | X |
| *Meles meles* | X | X | |
| *Nyctereutes procyonoides* | | X | |
| *Procyon lotor* | | X | |
| *Vulpes vulpes* | X | X | X |
| *Lepus europaeus* | X | X | X |
| **S** | **8** | **11** | **4** |
| **H** | **1,62** | **1,4** | **0,64** |
| **J** | **0,78** | **0,58** | **0,46** |

*3.2 Species diversity of counted animals*

In total we had 339 sighting events in 110 hours of counting. Species number and species diversity of counted animals differed considerably among the Exploratories. In the Schwäbische Alb only four species could be counted, whereas in Schorfheide-Chorin and Hainich-Dün eight and eleven species could be counted in total (Tab.1). The Shannon diversity and Evenness was lowest in the Schwäbische Alb, medium in Hainich-Dün and highest in Schorfheide-Chorin, although the overall species number of sighted animals was highest in the Hainich-Dün Exploratory.

*3.3 Abundance estimates of sighted species*

Due to a relatively low sample size we computed the counting indices by pooling the data for two counting sessions per species and Exploratory. The counting indices were computed for all observed species, but for comparison only the most abundant species were taken into account (Fig.3). We recorded the highest counting index for roe deer in all three Exploratories, ranging

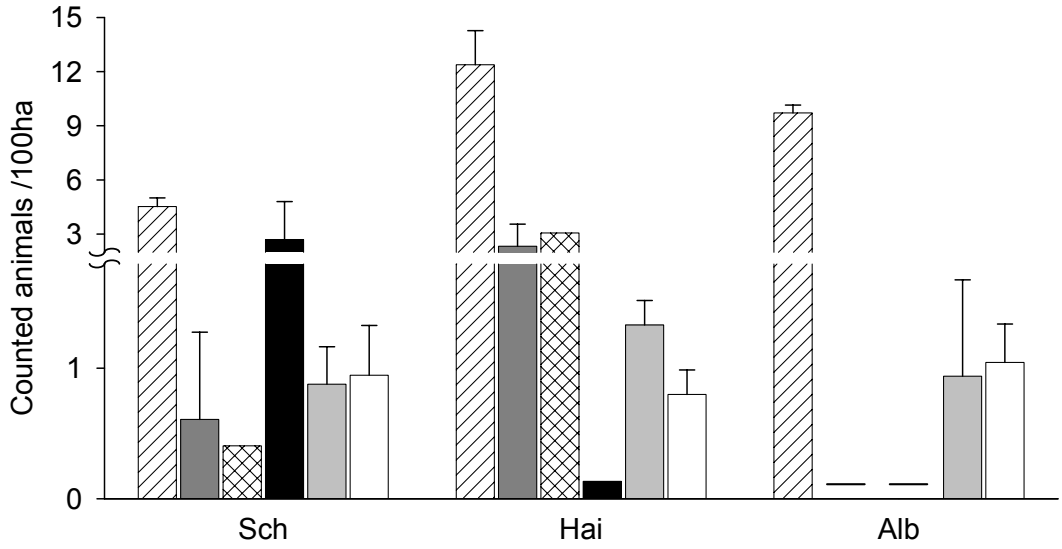


**Figure 3:** Counting indices of most abundant species in the Exploratories Schorfheide-Chorin (A), Hainich-Dün (B), and Schwäbische Alb (C). Roe deer is symbolised by hatched bars, fallow deer has dark grey bars, red deer is represented by cross hatched bars, wild boar has black bars, fox and hare are symbolised by light grey and white bars.

from 4.5 ind./100ha in Schorfheide-Chorin up to 9.7 ind./100ha in the Schwäbische Alb, and 12.4 ind./100ha in Hainich-Dün. Hence, we observed significantly more animals of roe deer in Hainich-Dün than in the Schwäbische Alb ($p < 0.05$), and Schorfheide-Chorin ($p < 0.01$). Red deer and fallow deer could not be seen in the Schwäbische Alb, but were present with low numbers in Schorfheide-Chorin (red deer 0.4 ind./100ha, fallow deer 0.6 ind. /100ha), and moderate numbers in Hainich-Dün (red deer 3.1 in./100ha, fallow deer 2.3 ind./100ha). However, the differences of counting indices for red deer and fallow deer between Schorfheide-Chorin and Hainich-Dün were not statistically significant. We had no sightings of wild boar in the Schwäbische Alb, but observed very low numbers of wild boar in Hainich-Dün (0.13 ind./100ha = one animal), and moderate numbers in Schorfheide-Chorin (2.7 ind./100ha). Since we only sighted a single animal in Hainich-Dün, it was not possible to test for significant difference between counting index of wild boar in Schorfheide-Chorin and Hainich-Dün.

Red fox and brown hare had equal numbers throughout the Exploratories with approximately 1 ind./100ha (red fox: Schorfheide-Chorin = 0.9 ind./100ha, Hainich-Dün = 1.3 in./100ha, Schwäbische Alb = 0.9 in./100ha; hare: Schorfheide-Chorin = 1 ind./100ha, Hainich-Dün = 0.8 ind./100ha, Schwäbische Alb = 0.9 ind./100ha).

*3.4 Distance sampling of roe deer*

By using the method of distance sampling, we were only able to compute an estimated abundance for roe deer. Counting data of other species were insufficient to get reliable estimates, and were therefore not included in this analysis. In total we used 252 sightings of roe deer for the distance sampling analysis, 47 in Schorfheide-Chorin, 145 in Hainich-Dün, and 60 in the Schwäbische Alb. The data were right truncated by 10% because of the limited number of observations in the right hand tail of the detection curve. Additionally, we applied another analysis in order to address the trough close to zero distance (Ward et al. 2004). This was necessary as the functions that DISTANCE fits to the data all assume the greatest probability of detection is for animals on the transect, resulting in a shoulder at zero distance (Buckland et al. 2001).

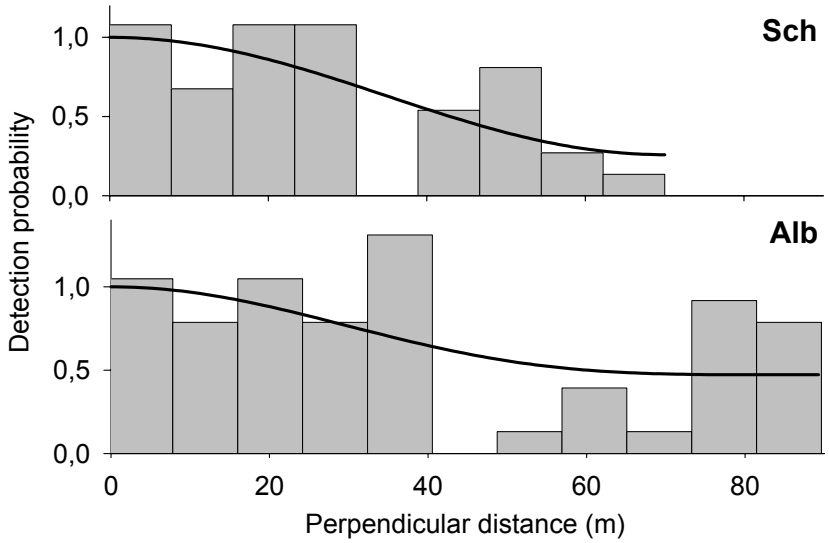


**Figure 4:** Detection probability plots (right-truncated by 10%, left truncated by 20m) for roe deer on the survey tracks in Schorfheide-Chorin (Sch), and the Schwäbische Alb (Alb). Grey bars are actual observations of roe deer, grouped at 0.5m intervals (Schorfheide-Chorin), and 0.7m intervals (Schwäbische Alb). The best model fit is represented by the black line.

**Table 2:** Estimates of roe deer density along the tracks in the Biodiversity Exploratories, associated errors, and the goodness of fit of the detection function. Aikaike´s Information Criterion (AIC) was used to select the best fit, and Chi² was used to determine the goodness of fit of the model

| Exploratory | Density estimate (animals/100ha) | 95% conf. interv. | AIC | Chi² | df | *P* |
|---|---|---|---|---|---|---|
| Schorfheide-Chorin | 4.25 | 2.43 – 7.42 | 351.65 | 10.55 | 7 | 0.16 |
| Hainich-Dün | 7.76 | 4.86 – 12.40 | 1130.56 | - | - | - |
| Schwäbische Alb | 6.67 | 3.81 – 11.69 | 503.25 | 18.65 | 8 | 0.02 |

Data were left truncated at 20m, so that the model was not constrained by the limited number of deer observed on or close to the counting transect. For roe deer counting data of the survey tracks in Schorfheide-Chorin and Hainich-Dün the best-fit detection model was a uniform key function with a single cosine adjustment term. Animal sightings in the Schwäbische Alb could be best explained by a uniform key function with a twofold cosine adjustment term (Fig.4). The density estimates derived by the method of distance sampling were entirely smaller than the estimates from the counting indices, with the difference being most distinct in Hainich-Dün (37%) and the Schwäbische Alb (30%), followed by a minor difference in Schorfheide-Chorin (5%) (Tab.2). According to the density estimates the encounter rate (number of countable animals/km) was 0.29 ind./km in Schorfheide-Chorin, 1.00 ind./km in Hainich-Dün, and 0.52 ind./km in the Schwäbische Alb. The detection function could only be computed for data from Schorfheide-Chorin and the Schwäbische Alb (Fig.4), whereas the Kolmogorov-Smirnov goodness-of-fit test (testing for an alternative model fit) was statistically significant in Hainich-Dün (K-S GOF Test, $t = 0.19$, $p < 0.001$), meaning that the detection function was not usable. Concerning the average group size of roe deer along the survey tracks, there were minor but non-significant differences between numbers of animals in a group of about 1.28 ± 0.1 in Schorfheide-Chorin, 1.24 ± 0.06 in Hainich-Dün, and 1.54 ± 0.1 in the Schwäbische Alb.

*3.5 Comparison between counting indices and harvest data*

By selecting hunting areas lying directly on the survey tracks or having a maximum distance to the tracks of 1km, 3 hunting areas in Schorfheide-Chorin, 18 in Hainich-Dün, and 9 in the Schwäbische Alb were included in the analysis. For direct comparison between counting and hunting data we pooled data along the hunting areas, and calculated a single value for each species per Exploratory.

Due to the absence of red deer, fallow deer and wild boar in the Schwäbische Alb, only data from roe deer and red fox could be included in this Exploratory. Wild boar comparison was

missing in Hainich-Dün as well. There was a significant positive relation between the number of shot animals/100ha and the counting indices ($R^2 = 0.6$, $p < 0.05$; Fig.5), whereas roe deer showed the largest differences between the Exploratories. The ratio between counted to shot animals of roe deer was 1.5 in Schorfheide-Chorin and the Schwäbische Alb, but was 3.3 in Hainich-Dün, suggesting that three times more individuals of roe deer were counted than shot in Hainich-Dün. Conclusively, by comparing all data of shooting rates and counting indices, more animals were counted than shot.

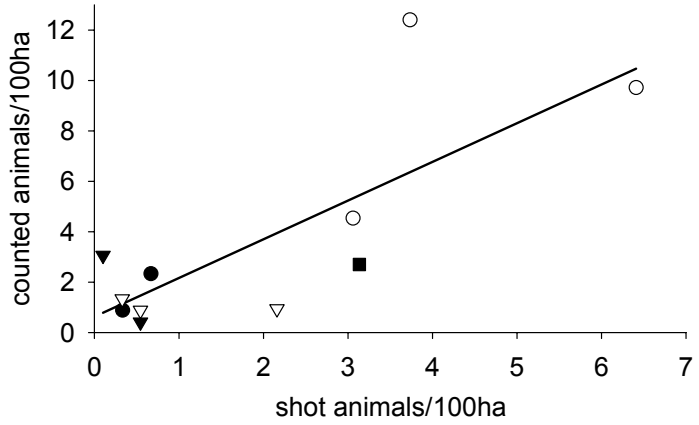


**Figure 5:** Relation between harvest rates and counting indices in all three Exploratories. Roe deer is symbolised by open circles, closed circles represent fallow deer, open triangles are red fox, closed triangles are red deer, and closed square is wild boar. Linear regression model is symbolised by black line.

*3.6 Habitat use of selected species*

Because of data restrictions it was not possible to compute the habitat selectivity index for all observed species. As with the counting indices, the most abundant species were taken into account. Since red fox was equally distributed throughout the habitats, brown hare was using only open areas (fields), and data on red deer were insufficient, we just used roe deer, fallow deer, and wild boar for this analysis. Roe deer showed preference for beech stands in Schorfheide-Chorin, whereas there was hardly any interaction with this habitat type in Hainich-Dün and the Schwäbische Alb. Additionally, open land was avoided in Schorfheide-Chorin and Hainich-Dün, but was preferred in the Schwäbische Alb. Roe deer showed no interaction with spruce/pine stands in Schorfheide-Chorin, and avoided this habitat type in the Schwäbische Alb and Hainich-Dün. There was little interaction with mixed stands in the Schwäbische Alb, but conifer/deciduous mixed stands were avoided in Schorfheide-Chorin and preferred in Hainich-Dün (Tab.3).

**Table 3**: Habitat selectivity indices of roe deer and fallow deer with sample size (brackets) in relevant Exploratories Schorfheide-Chorin (Sch), Hainich-Dün (Hai), and the Schwäbische Alb (Alb)

| | ***Capreolus capreolus*** | | | ***Dama dama*** | |
|---|---|---|---|---|---|
| | **Sch** | **Hai** | **Alb** | **Sch** | **Hai** |
| open land | -0.88 *(1)* | -0.31 *(15)* | 0.35 *(35)* | -1.00 *(0)* | 0.44 *(11)* |
| spruce/pine | 0.03 *(20)* | -1.00 *(0)* | -0.61 *(18)* | 0.78 *(7)* | -1.00 *(0)* |
| conifer/deciduous mix | -0.60 *(1)* | 0.57 *(12)* | 0.2 *(7)* | -1.00 *(0)* | 0.94 *(14)* |
| deciduous mix | 0.17 *(16)* | 0.15 *(38)* | 0.07 *(9)* | 0.10 *(2)* | 0.10 *(7)* |
| Beech/oak pure | 0.34 *(26)* | 0.04 *(110)* | -0.07 *(24)* | -1.00 *(0)* | -0.89 *(3)* |

Fallow deer avoided beech stands and preferred conifer/deciduous mixed stands and open land in Hainich-Dün. Because of small sample size, only preference for spruce/pine stands and minor preference towards deciduous mixed stands could be recorded in Schorfheide-Chorin. Wild boar was exclusively present in beech/oak mixed and pure stands in Schorfheide-Chorin, and, therefore preferred this type of habitat in this Exploratory.

# 4 Discussion

In our study we used the method of spotlight counting to monitor large mammals in the Biodiversity Exploratories, which considerably differed in composition of forest types. Portions of deciduous forest stands were larger along the survey tracks in Hainich-Dün since this area contained one of the largest coherent deciduous forest areas in Germany. Spruce forests were therefore rather uncommon in Hainich-Dün. However, pine forests represented large areas in Schorfheide-Chorin, and spruce forests were rather common and the Schwäbische Alb. Hence, these forest types had larger portions along the two latter survey tracks.

## *4.1 Species richness along the counting tracks*

Species number and diversity were lowest in the Schwäbische Alb, since several species were not present in this Exploratory. Although the survey track in Hainich-Dün yielded the highest number of overall species, the Shannon diversity was higher in Schorfheide-Chorin. We presume that this was due to the dominance of roe deer in Hainich-Dün. Out of the deer species, solely roe deer could be counted in the Schwäbische Alb, since red deer and fallow deer were not naturally distributed in this area (Görner and Hackethal 1988). As with the large deer species, there were no reported sightings of raccoon and raccoon dog in the Schwäbische Alb. As in the Schwäbische Alb, raccoon and raccoon dog were not observed along the survey track

in Schorfheide-Chorin, although they were evidently present in this area (hunting data). The reason for absence may have been either a low population density of these two species, or habitat characteristics along the track (brushy vegetation) which may have unfavoured the visibility of this two rather small carnivore species. The wild cat was only sighted in Hainich-Dün, because this threatened species is highly protected in the Nationalpark Hainich, and has been spreading out into the surrounding forest areas. Red fox and hare were almost equally distributed along the Exploratories, confirming that these two species are present all over Germany and large parts of Europe (Görner and Hackethal 1988).

*4.2 Differences in counting indices of selected species*

We only counted high numbers of wild boar in Schorfheide-Chorin, although this species was evidently present along the survey tracks in all three Exploratories (harvest 2007/08: Schorfheide-Chorin: 3.14 ind./100ha, Hainich-Dün: 2.25 ind./100ha, Schwäbische Alb: 1.56 ind./100ha). Harvest rates indicated that this species was more or less equally distributed throughout the study areas which is in line with other studies reporting that the occurrence of wild boar was supposedly unaffected by habitat parameters such as food availability and cover (Virgos 2002). We suggest that the actual sighting of wild boar was closely related to human disturbance, since the level of anthropogenic influence in the habitat differed considerably between the survey tracks in the Exploratories. The level of touristic activity and the network of roads and paths was highest along the survey track in the Schwäbische Alb, intermediate in Hainich-Dün, and lowest in Schorfheide-Chorin, although we did not collect quantitative data on that. Presumably, avoidance of wild boar to high levels of disturbance, may have repelled animals and led to very low sighting numbers in Hainich-Dün or no sighting in the Schwäbische Alb during the counting events. Indeed, the method of spotlight counting was proposed to be the wrong method for wild boar monitoring (Focardi et al. 2001), as thermal imaging provided more accurate data.

Regarding animal abundance of deer species, it was obvious that roe deer abundance exceeded fallow deer and red deer abundance four fold in Schorfheide-Chorin and Hainich-Dün. Differences in deer species abundances were presumably due to species specific harvest rates, growth rates, and local population fluctuation along the survey tracks. However, roe deer has the highest growth rates of all deer species (100% of female population/year (Stubbe and Stubbe 1990)), which may lead to very high population densities irrespective of moderate hunting pressure.

*4.3 Distance sampling analysis of roe deer counting data*

Analyses of roe deer counting data using distance sampling method turned out to be not as accurate as intended. Density estimates were exclusively lower than the actual counting indices along the survey tracks, which may be on the one hand due to data truncation in the DISTANCE program. However, data truncation on the left side of the detection curve is supposed to be necessary, because of roe deer avoidance of roads and tracks (Ward et al. 2004). We suggest that the counting indices could not have been an overestimation of real roe deer densities, but were rather an underestimation. Therefore estimated abundances of roe deer derived by DISTANCE were relatively imprecise. On the other hand the perpendicular distance to a sighted animal was estimated with the naked eye and grouped in 10m classes during the spotlight counting. It is likely, that this type of data collection was too coarse and the error was too high to create reliable results in the DISTANCE program. As a matter of fact the distribution of the detection probabilities indicate that estimating the distance to the sighted animal was insufficient, because of showing a lack of detections around 30m in Schorfheide-Chorin and 40m in the Schwäbische Alb (Fig.4). A more accurate ascertainment of the distance data probably would have increased the precision of the computed abundance estimates. In other studies distances to sighted individuals were measured by using a combination of thermal infrared locating and a mobile laser range finder to distinguish the actual distance (Focardi et al. 2002).

*4.4 Comparison between counting indices and harvest data*

Data on harvest rates and counting indices were positively related which indicated that monitoring using spotlight counting was a robust method to reveal differences in trends of population density (McCullough 1982, Acevedo et al. 2008). In average, the ratio of counted animals per shot animals was larger than one, meaning that more animals were counted than shot. This is due to the fact, that only the annual rate of population increment is planned to be harvested to gain a relatively stable population density. However, differences in harvest rates compared to counting indices appeared especially in roe deer. We conclude that in Hainich-Dün less roe deer were shot compared to a certain population density than in Schorfheide-Chorin and the Schwäbische Alb, because counting indices were rather an underestimation of real population densities.. Forest managers and private hunters are supposed to be differentially motivated to harvest animals in a varying amount (pers. comm.). Foresters try to decrease the damage caused by high deer numbers on young trees as much as possible to get sustainable growth rates of trees being important for high quality timber production (e.g. oak, maple, ash, and alder). On the other hand, a various number of private hunters are often motivated by having

a larger number of deer in the hunting area they are paying for, to satisfy the personal wish of high hunting success. Since hunting areas around the survey track in Hainich-Dün contained the highest portion of private hunting areas, this may be one reason for the observed low harvest rates. In Schorfheide-Chorin approximately 80% of the survey track was covered by federal forestry land, which held one of the lowest densities of large herbivores in the area. Thus, harvest rates of all deer species were highest in Schorfheide-Chorin. Finally, we suggest that harvest rates are very difficult to use for observing population trends of large herbivores, if motivation and pressure of hunting is not equal between different sites. Looking at harvest rates of wild boar, it appears that in Schorfheide-Chorin more animals were shot than counted (Fig.5). But due to the fact that only a certain portion of the actual population is authorised to be shot in the hunting season, we suggest that even relatively high counting numbers of wild boar in Schorfheide-Chorin did not fully represent the actual levels of wild boar abundance in this Exploratory.

### *4.5 Habitat use of roe deer and fallow deer*

Habitat use of roe deer and fallow deer largely differed between the Exploratories. One reason of habitat selection is supposed to be the amount of available food during winter, which mainly determines the quality of a certain habitat (Hofmann et al. 2009). Therefore, the amount and availability of winter food was likely to predict deer habitat use along our survey tracks. Open land represented winter crop fields or grassland containing moderate amount of food. Both deer species avoided this habitat in Schorfheide-Chorin. In Hainich-Dün fallow deer preferred, and roe deer avoided open land. Contrary, roe deer preferred this type of habitat in the Schwäbische Alb, where fallow deer was not present. Hence, fallow deer tended to use the available food in open land more intense, and roe deer seemed to be repelled in Hainich-Dün. This is in line with an Italian study which reported fallow deer to highly use open habitats (Focardi et al. 2002).

In Schorfheide-Chorin pine stands were stronger preferred by fallow deer than by roe deer, whereas spruce was avoided by both species in Hainich-Dün and by roe deer in the Schwäbische Alb. We suggest that spruce stands contained very little winter food supply, but pine forests in Schorfheide-Chorin had very high amounts of usable food plants (e.g. blackberry, raspberry), which were however more intensively used by fallow deer. Conifer/deciduous mixed stands contained very little winter food supply in Schorfheide-Chorin (pine/beech), resulting in habitat avoidance of both species. However, in Hainich-Dün conifer/deciduous mixed stands seemed to attract both deer species. It remains unclear, if high winter food supply or increased coverage in this type of habitat was the reason for the observed pattern. Beech/oak pure stands were

exclusively avoided by fallow deer, whereas roe deer showed no interaction in Hainich-Dün and the Schwäbische Alb, but showed attraction to this kind of habitat in Schorfheide-Chorin. Individuals of roe deer showed the same pattern of using deciduous oak forests in a Mediterranean study area (Focardi et al. 2002). Pure deciduous forests have little amount of winter food compared to e.g. pine stands. Nevertheless, roe deer is likely to use parts of young trees such as buds and branches for feeding, and therefore used this habitat more than fallow deer.

Conclusively, it seemed that fallow deer was partly able to repel roe deer from habitats where both species occurred, because elsewhere it has been shown that species specific grazing has the potential to modify the habitat structure in favour of one species (Focardi and Tinelli 2005). Roe deer was reported to be a very selective feeder (Tixier et al. 1997), it was supposed to be more effected by dietary competition (Latham et al. 1999), and thus used habitats which were avoided by fallow deer in our study maybe due to suboptimal food availability. Fallow deer was supposed to live in heterogeneous environments through age and sex dependent habitat selection and adaptive modifications of aggregation patterns (Apollonio et al. 1998). Furthermore, this species was even reported to have a high plasticity to use different habitats in a changing environment (Thirgood 1995), and contributed to the decline of roe deer populations due to fragmentising the distribution of suitable habitats for roe deer (Focardi et al. 2006). Hence, we suggest that fallow deer in our study showed a stronger potential to use habitats with high winter food supply, and thereby repelling roe deer to suboptimal habitats like beech and oak forests.

However, it may be difficult to conclude patterns of habitat use of deer species taking data from spotlight counting, because these data were collected over a period of several hours and nights (McCullough 1982). This may have led to biased data which not fully represent an authentic habitat use of the observed species. Finding animals in a certain habitat type during a small number of nights may not necessarily give information about a general habitat use of this species. Furthermore, animal activity may be different during the counting event. Beside this, brushy vegetation may have reduced visibility along parts of the survey tracks to a minimum level so that data were not reliable as such in this kind of habitat.

*Conclusion*

Spotlight counting as a method for monitoring large mammal species has been shown to be an applicable method over large areas of the Biodiversity Exploratories. Because of its ease of handling and cost effectiveness it holds high potential for further monitoring programs where an

index of relative animal abundance is wanted. However, to get more precise density estimates, distance measurements should be recorded more accurately. Visibility estimates predicted the counting area, and errors may lead to biased estimates of relative animal abundance. A more precise measure of distance to the counted animal does not necessarily improve the counting indices, but may increase the precision of applied models in the distance sampling program. Although being rather cost intensive, mobile laser range finders seem to be the best solution for this purpose. However, we suggest that counting indices reflected trends in population densities, since they were positively related to harvest rates of selected species. Lower numbers of animals counted than shot can be explained by underestimation of counted animals due to reduced sighting. Disproportionately high counting numbers compared to shooting rates can only be caused by a low hunting pressure, because counting indices cannot be an overestimation of real population densities. To uncover trends of population development over a period of time, monitoring surveys have to be repeated using the same method and standardized tracks over several years. By doing so, we suggest that data derived by replicated spotlight counting may be more accurate than data on harvest rates.

In terms of habitat use spotlight counting data predicted patterns of habitat segregation between roe deer and fallow deer. But as data were created over a short period of time, results were probably not as reliable as cumulative methods such as faecal pellet group counts. Because they gather data over several weeks or months irrespective of any disturbance due to counting, faecal pellet group counting methods should be preferred if detailed information about habitat use is desired.

# HABITAT USE OF LARGE UNGULATES IN NORTH EAST GERMANY IN RELATION TO FOREST MANAGEMENT

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## Abstract

Estimating large herbivore density has been a major research focus in recent decades. However, previous studies dealing with monitoring of ungulates mostly focused on determining animal abundance, and did not interpret animal distribution in relation to habitat parameters. We surveyed large ungulates in the Biodiversity Exploratory Schorfheide-Chorin using faecal pellet group counts. This allowed us to explore the link between ungulate abundance, habitat use, and browsing damage on trees in a region with several types of forest, including unmanaged and age-class beech forests and age-class pine forests. We observed roe deer and fallow deer abundance to be negatively correlated with large tree cover, and positively correlated with the cover of small shrubs (*Rubus spec., Vaccinium spec.*), as well as winter food supply. Habitat use of roe deer and fallow deer derived by counting faecal pellet groups revealed preference to mature pine forests with high cover of edible plants, and avoidance to deciduous forests, which is explained by varying distribution of high quality food resources. The response of deer towards understory cover differed between roe deer and fallow deer at high cover percentages. Browsing damage on coniferous trees was not explained by high deer abundance. Browsing was higher in deciduous trees, but solely beech saplings suffered less damage than other deciduous trees at low roe deer density. Because of being a concentrate selector, we suppose roe deer to affect tree diversity by selectively feeding on species containing high quality ingredients. We conclude that roe deer abundance needs to be adjusted by hunting to a sustainable level to permit forest regeneration on a large spatial and temporal scale. This adjustment needs to take into account the proportions of young tree saplings and alternative food source in the ground vegetation. Our findings may be applicable to other North-East German forest landscapes including mature pine stands and differently managed deciduous forests.

**Keywords: large ungulates, faecal pellet group count, forest management, habitat use, browsing damage**

# 1 Introduction

The impact of large ungulate species, such as deer, on the vegetation structure due to browsing, bark stripping, and fraying is apparent over large areas of northern temperate forests. It has been proposed that population density of large herbivores rising above the carrying capacity of an environment can change plant communities (Mysterud 2006), and thus, can have an immense effect on biodiversity and ecosystem functioning (Trdan and Vidrih 2008). Thus, monitoring large ungulates is a major component of wildlife supervision (Buckland et al. 1996) to improve the development of appropriate management strategies (Doerr et al. 2001), and to reduce negative effects caused by inadequate animal density to an economically acceptable level. Damage effects may not be linked exclusively to a high population density of large herbivores, but also to attributes of plant species. In certain habitats, site related factors such as hiding cover or snow may have an additional influence on the degree of damage (Gill 1992a). Nevertheless, the effect of varying densities of large herbivores is thought to be one of the important variables in affecting habitat changes. Hence, there has been the need for density estimation methods connecting site related factors and animal population density, as precise data are still unavailable (Gill 1992a).

The logistic and financial effort required to estimate real population density of large mammal species on a regional scale is very high. Thus, various alternative methodologies to estimate relative abundance of large herbivores have been developed (Putman 1984, Mysterud et al. 2007). Direct census methods are based on animal observations at the actual time of the survey, and are therefore more prone to sample errors when species are highly mobile and vegetation is very dense (Smart et al. 2004). Indirect census methods are often based on faecal pellet group counts which integrate over larger time periods and are unaffected by habitat visibility (Bailey and Putman 1981, Putman 1984, Hemami et al. 2005). The faecal accumulation rate (FAR) (Smart et al. 2004) requires initial clearing of the survey plots to estimate the number of accumulated pellet groups by knowing the species specific defecation rates (Mayle 1996). The FAR method has a low potential for bias and is more efficient than other methods when their overall precision is compared (Campbell et al. 2004).

Former studies applying census methods of large ungulates have often focused on animal abundance alone, without linking it to habitat characteristics. However, such links are necessary to elucidate ultimate reasons for habitat use and occasional damage on plants. The question remains whether high animal density is only caused by increased resource availability, or whether it is also significantly affected by other factors such as habitat heterogeneity. Furthermore, it is unclear whether high animal abundance results in locally increased plant

damage, and whether patterns of damages vary across habitat types. Therefore, it is crucial to link information about relative animal density with data on habitat attributes and browsing damage.

Over the next decades, forest areas in Germany will considerably change due to modern silvicultural practice. Today, pine (*Pinus sylvestris*) monocultures represent up to 70% of total forest area of the federal state Brandenburg in North East Germany (MLUV 2005), but the long-term goal of forest management in North East Germany (MLUR 2004) is to transform these monocultures into more natural beech or mixed deciduous forests. This indeed will have a high impact on the suitable habitat for many forest living animals. However, it is not known to what extent structural changes in habitat attributes affect the abundance of large herbivores and their cause on vegetation structure. It is therefore necessary to compare different forest types to assess species specific habitat use and to clarify the value of near natural and managed forest habitats for large herbivores. Thus, we need to study the relationship between animal presence and a broad variety of habitats to project possible scenarios of individuals' and species' response to changes in forest management.

Here, we present a monitoring program for large ungulates conducted in the Biodiversity Exploratories at the Schorfheide-Chorin site in North East Germany. The experimental setup of the Biodiversity Exploratories allows for studying the link between relative animal abundance and different forest types, containing a high number of research sites in various habitats, ranging from near natural to human made forests. We used a strip transect survey with the faecal accumulation rate (FAR). Additionally, we unravel the link between estimates of relative animal abundance, and habitat use, by identifying patterns of browsing damage on the survey plots.

In particular, we address the following questions: 1. Which pattern of relative large ungulates abundance and distribution can be derived from faecal pellet group counting (FAR) in relation to different management type and habitat characteristics? 2. Which habitats are preferred by the ungulate species? 3. Is browsing damage correlated to high ungulates abundance?

# 2 Material and Methods

## *2.1 Study site*

Faecal pellet group counts were conducted in the Biodiversity Exploratory Schorfheide-Chorin (N 52° 54´; E 13° 52´) (Fig.1) (www.biodiversity-exploratories.de). The study area is situated within the Biosphere Reserve "Schorfheide-Chorin" and is characterised by a post glacial landscape with a yearly precipitation of 520-580mm. Most of the forest area is characterised by beech stands (mixed with hornbeam, mountain oak, and little-leaf linden), pine beech mixed stands (dense lower tree layer of beech, loose canopy layer of pine), as well as monocultures of pine (with a dense groundcover of *Rubus spec., Vaccinium spec.*). The dominant large ungulate species in this regions are red deer (*Cervus elaphus*), fallow deer (*Dama dama*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*), but occasionally moose (*Alces alces*) are observed, too.

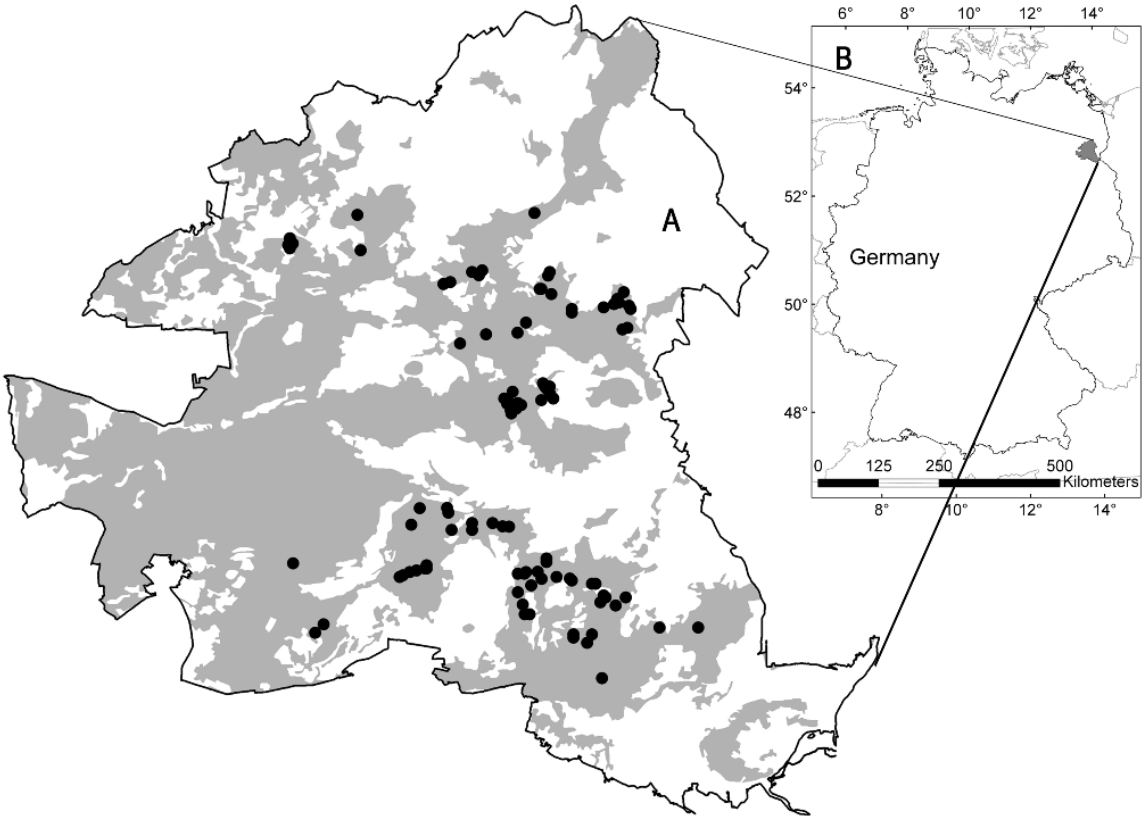


**Figure 1:** Location of the Biodiversity Exploratory Schorfheide-Chorin (A) in Germany (B). Survey plots for faecal pellet group counts are symbolized by black dots, with forests marked by grey areas.

We selected 97 study plots with an minimum distance of 200 m by choosing forest types according to their main tree species, forest age, and forest management, ranging from near-natural to intensively managed status (Tab. 1). In the study area near natural forests were represented by unmanaged beech stands containing old grown trees (> 50 years) with a low

amount of deadwood. Managed forest sites were represented by age-class forests that differed in the identity and age of the dominating tree species. Beech forests were categorised as managed old timber (> 50 years) with moderate deadwood and little understory vegetation, and as thicket stands (< 40 years) with little deadwood and dense shrub cover. Oak and beech-oak mixed forests contained managed old timber (> 50 years) having a moderate understory vegetation of herbs and shrubs. Pine-beech mixed forests were almost even aged, contained high deadwood cover, and were free of understory vegetation. Old timber pine forests contained little deadwood and a dense groundcover of *Rubus spec.* and *Vaccinium spec.*. Finally, the most human made forest type found in this area were pine forest with young timber or pole wood and were characterised by close standing monocultures with high deadwood cover and very little understory vegetation (Tab.1).

**Table 1**: Land use categories, number of plots, and forest type with corresponding age for faecal pellet group counting in the Biodiversity Exploratory Schorfheide-Chorin. Plot attributes are represented by stand density (mean ± SE of number trees/ha), cover of deadwood, and winter food supply (mean ± SE of kg dried substance/ha) characterising all edible plants during winter.

| Forest type | Land use | Number of plots | Age | Stand density | Cover of deadwood | Winter food supply |
|---|---|---|---|---|---|---|
| Beech unmanaged | 1 | 5 | >50y | 162.0 ± 32.6 | 2.2% | 3.8 ± 1.9 |
| Beech old timber | 2 | 17 | >50y | 289.4 ± 48.8 | 5.4% | 17.2 ± 7.3 |
| Beech thicket | 3 | 16 | 10 – 20y | 140.6 ± 18.7 | 2.5% | 46.6 ± 7.9 |
| Oak old timber, beech oak mix | 4 | 16 | >50y | 341.3 ± 53.7 | 3.1% | 33.9 ± 12.6 |
| Pine beech mix (old timber) | 5 | 13 | >40y | 494.6 ± 73.4 | 6.8% | 12.7 ± 6.8 |
| Pine old timber | 6 | 14 | >40y | 1841.8 ± 195.3 | 2.8% | 127.6 ± 9.7 |
| Pine young timber, pole wood | 7 | 16 | 5 – 20y | 377.9 ± 31.4 | 8.2% | 33.4 ± 8.1 |

*2.2 Explanatory variables*

We selected six explanatory variables for correlation analyses and stepwise linear regression model of faecal pellet group counting data. The land use was determined by the identity and age of dominant tree species, and the management status. The mean understory visibility in meter was estimated as a measure of thickness of the understory vegetation on the survey transect in November 2008, resulting in class one (100-75 m), two (75-50 m), three (50-25 m), and four (25-10 m). On a fixed square of 20 x 20 m near the pellet counting transect coverage of trees (> 10 m) and small shrubs (near forest floor) was estimated in five percent classes during the

previous summer in 2007. In particular, small shrubs (winter-green, winter-bald) were selected by taking all species yielding more than 60kg dry mass/ha at 50% coverage (e.g. *Rubus spec., Ribes spec., Vaccinium spec.*). Winter food supply for large ungulates was estimated as kg dry mass/ha using coverage data of all edible plants and categorization commonly used for determining habitat quality of forest habitats (Hofmann et al. 2009).

*2.3 Ungulate species abundance and habitat selectivity*

We used pellet group counting to assess the relative abundance of different ungulate species. In November 2008, right after leaf fall, we established one fixed transect of 2 x 100 m on each of the 97 study plots and removed all faecal pellets. When possible we avoided deer passes crossing the transects. We then counted the pellet groups two times in the middle of January and March 2009 and again removed all pellets in January 2009 to ensure similar starting conditions as in November 2008. Two people counted independently all pellet groups twice per transect, and values were corrected to gain one pellet number per species and plot. Only pellet groups were counted that had more than five single pellets inside the transect (Tottewitz et al. 1996). Pellet groups were assigned to individual species in the field (Bang et al. 2006).

We calculated an index of relative animal abundance for each species based on pellet groups for January and March separately, and for the pooled data as:

D = pellet groups per ha*100/(decay [days]*daily defecation rate [pellet groups per day]) (Mayle et al. 2000).

The decay time of pellets was represented by the number of days from the initial transect clearing until the counting event. We used the following daily defecation rates (pellet groups per day) of different ungulate species: 19 in red deer , 24 in fallow deer , 14 in roe deer , and 4.5 for wild boar (Tottewitz et al. 1996).

To further quantify the preference of ungulate species for certain habitats, habitat selectivity was computed for each of the major habitat types listed in Table 1 using all survey plots in the Exploratory. We computed habitat selectivity as Jacobs index for roe deer and fallow deer because of being most abundant and almost equally distributed. The Jacob index ranges from -1 indicating avoidance to +1indicating preference for a certain habitat type (Jacobs 1974).

*2.4 Browsing damage*

To assess the effect of ungulate species on vegetation, the browsing damage on tree species was recorded on a subset of 44 survey plots in summer 2008 where data of relative ungulate abundance was recorded during the following winter. We used two 25 $m^2$ areas and recorded browsing damages on all tree species from seedlings to young trees having a diameter smaller than seven centimetres. Data on browsing damage was obtained by pooling old and new damages on terminal and lateral branches of all plants for each species. For further analysis we computed the relative browsing damage (%) of beech, other deciduous trees, and pine in relation to (1) all observed trees and (2) all observed trees per species group.

*2.5 Statistical analyses*

Data were analyzed statistically with SPSS 15.0 and SPLUS 6.1. We used a square root transformation to reach normality and variance homogeneity of the counting data. The Pearson correlation coefficient, one way ANOVA, and multiple linear regression with stepwise model selection based on Akaike's information criterion (AIC) were used for analysing the influence of forest characteristics on animal abundance. The land use categories were not included in the stepwise linear regression model. ANOVAs were applied to compare means of counting data between different times of the year, habitat types, and cover classes on the survey plots. Furthermore linear regression was used for analysing data on browsing damage and deer density.

# 3 Results

## *3.1 Faecal pellet group counting*

In total we counted 1035 faecal pellet groups throughout the winter 2008/09, with significantly more pellet groups in January than in March 2009 (Tab.2). This translated into a higher animal abundance across all species in January compared with March ($p < 0.01$). Roe deer and wild boar were the most abundant species, followed by fallow deer, and red deer (Tab.2).

**Table 2**: Sum of faecal pellet groups (PG) and relative animal abundance (mean ± SE, individuals per 100 ha and day) on the plot scale for the most abundant species in January, March, and whole winter. ([a] All species include other faecal pellet groups from moose and sheep)

| | **January** | | **March** | | **whole study** | |
|---|---|---|---|---|---|---|
| | Sum PG | Ind./100 ha | Sum PG | Ind./100 ha | Sum PG | Ind./100 ha |
| Roe deer | 291 | 15.2 ± 2.3 | 97 | 6.8 ± 1.3 | 386 | 11.7 ± 1.8 |
| Fallow deer | 257 | 7.9 ± 1.8 | 147 | 6.0 ± 1.7 | 402 | 7.1 ± 1.7 |
| Red deer | 67 | 2.5 ± 0.4 | 36 | 1.9 ± 0.6 | 103 | 2.3 ± 0.4 |
| Wild boar | 83 | 13.1 ± 1.9 | 49 | 11.5 ± 2.9 | 131 | 12.4 ± 1.6 |
| All species[a] | 702 | 25.5 ± 3.5 | 333 | 16.6 ± 3.3 | 1035 | 21.9 ± 3.3 |

## *3.2 The effect of forest characteristics on ungulate abundance and habitat selection*

Overall, animal abundance of all species was higher in pine forests than in deciduous forests (Fig. 2A). In addition, animal abundance increased with winter food supply and cover of small shrubs, but decreased with the cover of large trees (Fig.2B-D). Abundance of all species could be best explained by the combination of cover of large trees and small shrubs in the complete study period (26%). Some of the explanatory variables were correlated among each other. For instance, we observed a higher cover of small shrubs, higher winter food supply, but lowest coverage of large trees in mature pine stands ($p < 0.05$) although not being intensively managed. Therefore, stepwise multiple regressions tested for the relative influence of forest characteristic on animal abundance in a joint analysis. Thereby, we identify differences of individual species of ungulates in their response to forest characteristics.

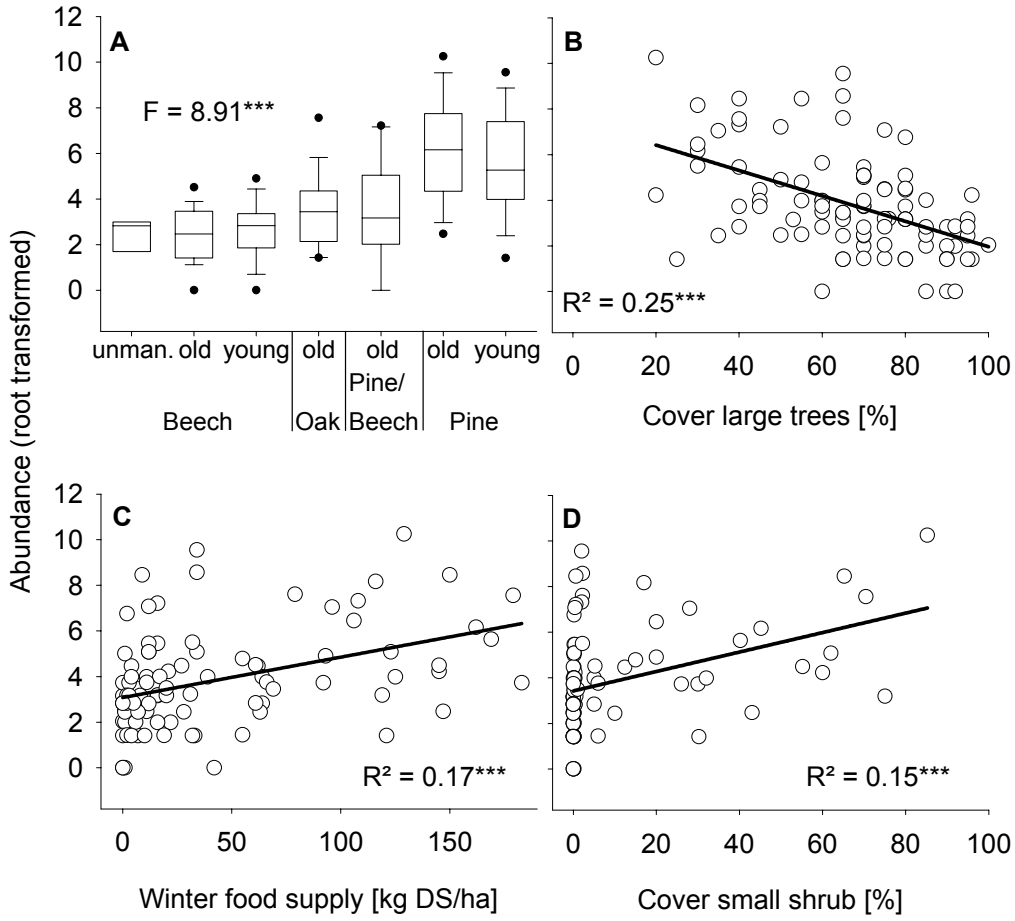


**Figure 2:** Relative animal abundance (root transformed) of all species derived by faecal pellet group counts depending on land use classes (A), cover of large trees (B), winter food supply (C), and cover of small herbs (D). The variance ratio F from the ANOVA and explanation coefficients $R^2$ form linear regressions are indicated.

Roe deer abundance was highest in old timber pine forests ($p < 0.05$), and therefore it preferred old pine timber stages (Fig. 4). Accordingly, roe deer strongly avoided unmanaged beech, old beech, and old oak forests and less strongly pine beech mixed and young beech forest. In addition, roe deer abundance increased with winter food supply (r = 0.5***), and cover of small shrubs (r = 0.5***) whereas it decreased with the cover of large trees (r =-0.5***) and understory visibility (r = -0.3***). For understory visibility, lowest abundance occurred at highest visibility (100-75 m), but did not differ among the lower visibility classes (Fig.3). Combination of large tree cover and small shrub cover explained roe deer variance in January (33%) and the whole study period (37%), whereas variance in roe deer abundance in March was best explained by the distribution of winter food supply alone (33%) (Tab.3).

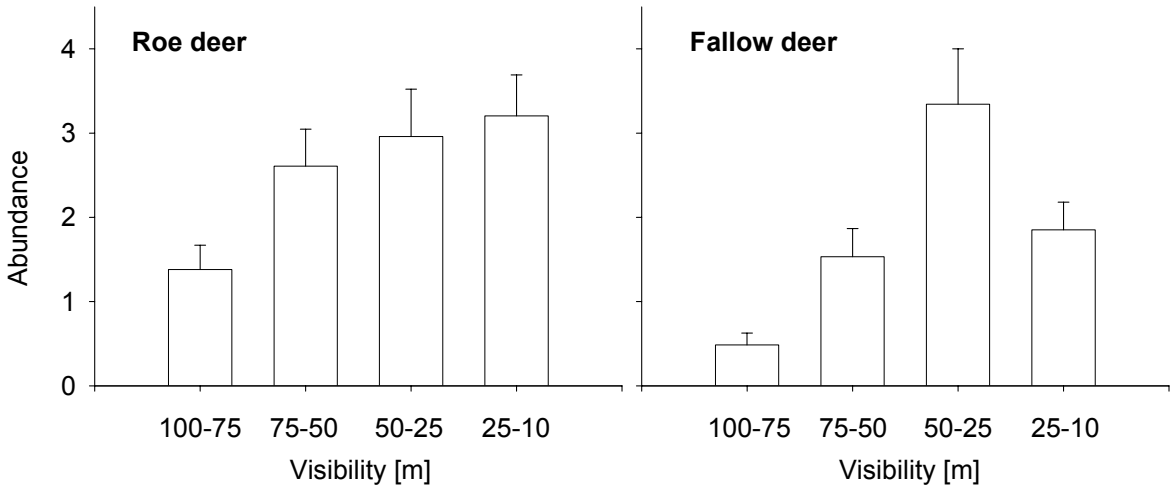


**Figure 3:** Relative animal abundance depending on total cover (visibility) on the survey plots (represented by visibility in meters) for roe deer and fallow deer.

**Table 3**: Minimal adequate models from multiple linear regression with stepwise model selection based on AIC on the relative animal abundance (animals per 100 ha and day) and winter food supply (WFS), cover of large trees (CovTree), and cover of small shrubs (CovShrub), in recorded species for January, March, and throughout winter ([a] All species include other faecal pellet groups from red deer, wild boar, moose and sheep, [b] explanation-coefficient, [c] level of significance, [d] F statistic)

| Animal abundance | explanatory variables | $R^2$ | P[c] | F[d] | AIC step |
|---|---|---|---|---|---|
| **January** | | | | | |
| Roe deer | CovTree+CovShrub | 0.21 | < 0.001 | 22.22 | -285.7 |
| Fallow deer | CovTree | 0.18 | < 0.1 | 8.65 | -302.4 |
| All species[a] | CovTree+CovShrub | 0.25 | < 0.001 | 13.15 | -282.6 |
| **March** | | | | | |
| Roe deer | WFS | 0.31 | < 0.001 | 46.22 | -333.8 |
| Fallow deer | CovTree | 0.2 | < 0.001 | 16.22 | -334.9 |
| All species[a] | WFS+CovTree | 0.25 | < 0.001 | 13.47 | -277.9 |
| **Throughout winter** | | | | | |
| Roe deer | CovTree+CovShrub | 0.28 | < 0.001 | 26.76 | -322.8 |
| Fallow deer | CovTree | 0.19 | < 0.001 | 14.46 | -330.0 |
| All species[a] | CovTree+CovShrub | 0.29 | < 0.001 | 15.98 | -308.8 |

Fallow deer abundance was higher in pine forests of young and old age than in managed and unmanaged deciduous forests ($p < 0.05$). This species showed a stronger preference towards old timber pine stands than roe deer. Pine beech mixed stands were not as strongly avoided by fallow deer as in roe deer. However, we observed strong avoidance towards all deciduous forest types in fallow deer (Fig.4). As with roe deer, fallow deer abundance increased with winter food supply (r = 0.2**) and decreased with cover of large trees (r = -0.4***) and with understory visibility (r = -0.3***). Different to roe deer, fallow deer responded less strong to winter food supply, and did not correlate with small shrub cover. Also in contrast to roe deer, fallow deer abundance peeked at an intermediate visibility of 50-25 m and was significantly lower in the lowest visibility class (Fig.3-B). Cover of large trees explained fallow deer presence in January (10%), March (15%), and the whole study period (14%) (Tab.3).

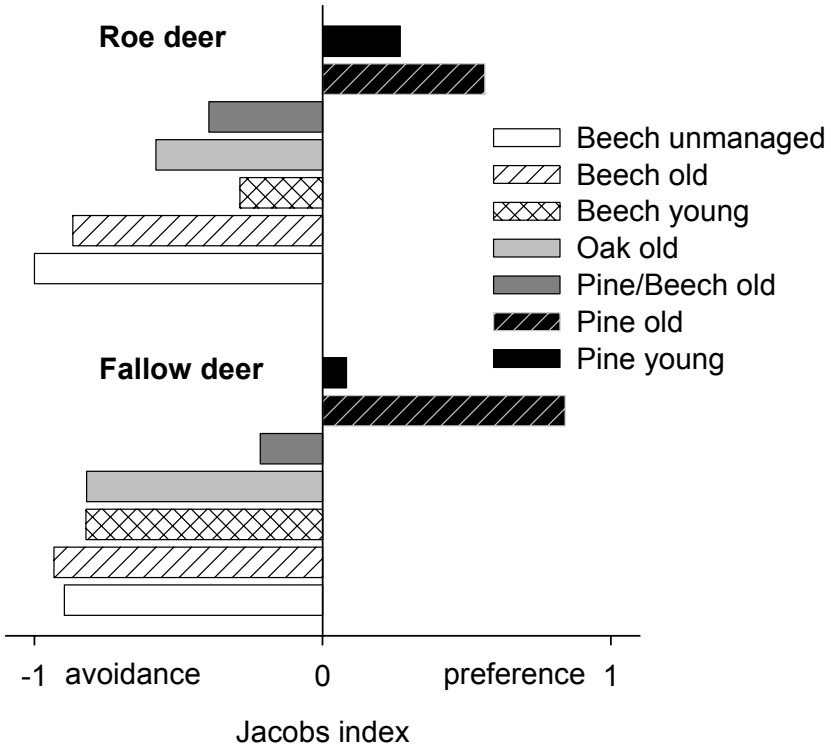


**Figure 4:** Jacobs indices showing preference (positive values) and avoidance (negative values) of different forest types by roe deer and fallow deer derived from faecal pellet group counting during winter 2008-09.

For red deer abundance, except for a negative correlation with total understory visibility (r = -0.3**) in March, we could not find any other effect of forest type or forest structure, possibly because of the overall low abundance of this species. Finally, wild boar did not respond

to any forest characteristics, and consequently did not show any habitat preference, indicating the broad ecological niche of this species.

*3.3 Browsing damage*

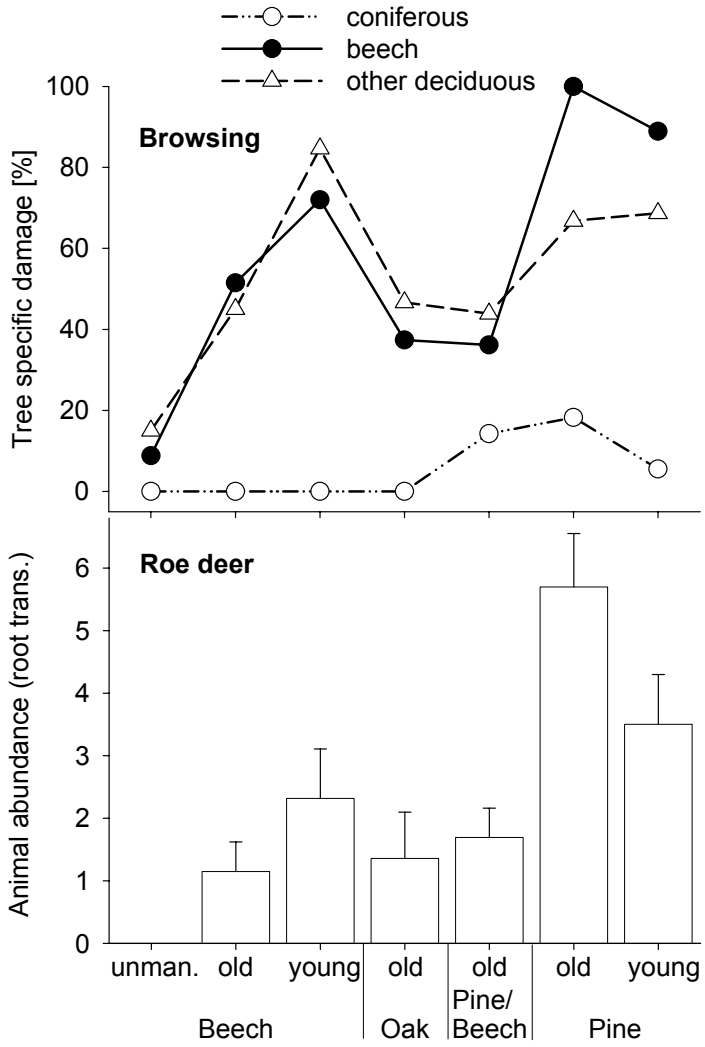


**Figure 5:** Roe deer abundance (root transformed for whole study period) in differently managed forests (bottom) and species specific browsing damage on coniferous trees, beeches, and other deciduous trees in the land use categories (top).

Browsing damage differed between tree species. In relation to all browsed trees observed damage was significantly lower on young pine trees (13.7%) than browsing damage on beech (36.6%) and other deciduous trees (49.6%) ($p < 0.01$). In relation to the number of all occurring tree seedlings per species and land use category young trees of pine suffered higher browsing damage in pine stands and pine beech mixed forest than in deciduous forest stands. We also observed a higher relative damage on beech seedlings in mature pine stands (100%) than in age

class forests of beech (60%). More than half of all other deciduous trees than beech were damaged in all forests except in unmanaged beech stands (15%) (Fig.5).

Additionally, relative browsing damage on beech trees in relation to all observed beech seedlings increased with increasing roe deer abundance across the land use categories (January: $R^2 = 0.85^{**}$, March: $R^2 = 0.56^{*}$, whole winter: $R^2 = 0.81^{**}$). As with young beech trees, other deciduous trees suffered higher relative browsing damage with increased roe deer abundance (January: $R^2 = 0.61^{*}$). However, no such relationship between browsing damage on pine trees or all tree species and animal abundance was found in any other of the ungulate species.

# 4 Discussion

## *4.1 Abundance estimates and habitat characteristics*

Animal abundance derived by faecal pellet group counts resulted in high numbers compared to other abundance estimates. In a comparative survey using spotlight counting in the forest area Chorin in March 2009 (unpublished data) we revealed average animal sighting density to be 16% lower than estimates form faecal pellet group counts in the same area. However, observed pellet numbers may be disproportionally high on a local scale due to attracting effects of the habitat. A reliable estimate of ungulate abundance can only be made by computing the average animal density of a sufficient number of survey plots on a large area of several thousand hectares.

Roe deer abundance was highly dependent on the availability of high quality food during winter, which was more pronounced at decreased large tree cover. This finding is in line with other studies on roe deer reporting a strong relation to high food availability and understory cover (low visibility) (Tufto et al. 1996). Fallow deer abundance was inversely related to large tree cover, which we presume to be caused by increased growth of feeding plants due to high light availability (von Oheimb and Härdtle 2009). Besides, fallow deer was reported to use different forest habitats for feeding owing to its high plasticity of habitat use in changing environments (Thirgood 1995). Therefore, fallow deer abundance may not only be connected to winter food supply in forest habitats, because than this variable would have been included in the stepwise regression model. Red deer abundance was only negatively correlated with stand visibility, as it was previously shown that red deer used replanted forests more than old closed-canopy stands (Catt and Staines 1987). Replanted forests with dense shrubby vegetation seemed to provide food and cover for this ungulate species. Wild boar showed no interaction to any explanatory variables and thus our results are in accordance with other studies that indicated the broad ecological niche of wild boar (Virgos 2002).

We suggest that the variation of habitat attributes between the forest types was an ultimate factor determining relative animal abundance of deer species. Changing management strategies in forest habitats can have an effect on canopy cover, and therefore may influence the amount of edible plants on the forest floor altered by increased light availability (Battles et al. 2001). In our study some forest types had a lower canopy cover on the survey plots compared with others which may not necessarily be connected to high management intensity. Reduced canopy cover may have enhanced the cover of small shrubs and herbs on the forest floor, and therefore the level of winter food supply. Mature pine forests yielded the highest estimates of deer abundance, which was due to the highest coverage of small shrubs. Hence, this forest type represented an optimal habitat for deer in terms of food availability during winter. But mature pine stands did not undergo an intensive forest management in the past decades, and represent a common forest type in the area of the Schorfheide-Chorin. In comparison, young beech and pole wood stands of pine were intensively managed, but did not contain high ungulate abundances due to low food availability.

*4.2 Detailed habitat use of roe deer and fallow deer*

Roe deer and fallow deer clearly preferred mature pine stands to all other forest types, and showed a strong avoidance of unmanaged beech forests, providing neither food resources nor shelter at all. Roe deer preferred mature pine forests. We explained roe deer abundance to be determined by the cover of small shrubs and winter food supply. Hence, this is supposed to be the main factor predicting animal presence, as food availability was highest in mature pine stands. However, roe deer occurred more often in deciduous forests like young beech stands than fallow deer. As tree saplings also account for the value of winter food supply, we suggest that roe deer is able to shift to other food resources than ground vegetation. The absence of ground vegetation when habitats other than pine forests are occupied may be compensated by consuming parts of young trees. Fallow deer showed maximum preference to mature pine forests. Additionally fallow deer avoidance towards deciduous beech and oak forests was stronger than for roe deer. Beside increased ground vegetation in pine forests, high abundances of bryophytes in mature pine stands could be a factor determining fallow deer distribution. The productivity of this ground vegetation is very high, and it may act as an additional food resource (Nilsson and Wardle 2005).

Understory visibility had different effects on roe deer and fallow deer abundance (Fig.3), which we explain by fluctuating climate factors and food availability. Former studies have documented that deer may use high cover to reduce cold stress (Mysterud and Ostbye 1995),

and lowering wind speed was supposed to be the most important factor using thermal shelter during winter. In particular, smaller deer are more susceptible to cold stress due to different surface volume ratios (Mysterud and Ostbye 1999), which may indicate an adaption to reduce loss of body temperature due to wind chill in the smaller roe deer. Furthermore, roe deer may feed on shoots and buds of young trees when ground vegetation is rare on plots with low visibility due to shading.

*4.3 Browsing Damage in relation to animal density*

As damage on pine trees was not strongly related to roe deer abundance, it seems that a high amount of ground vegetation and few young deciduous trees in mature pine stands prevented young pine trees from increased browsing damage. Although not being very abundant in pine forests, young deciduous trees suffered higher specific browsing damage than pine trees (Fig.5). We explain preference for young deciduous trees in pine forests with higher energy content and better taste for deer. Former studies found alternative food availability to affect the amount of winter browsing on spruce trees by roe deer (Welch et al. 1991, deJong et al. 1995). In mature pine stands, small shrubs (*Rubus spec., Vaccinium spec.*) are supposed to have maximum food quality and have been reported to be highly consumed by roe deer (Moser et al. 2006). We suggest that these plants played a major role for roe deer feeding acting as alternative food in mature pine stands and thus preventing pine sapling from increased browsing despite high animal density.

Deciduous forests contain very little ground vegetation which in return enhanced deer browsing on tree saplings (Moser et al. 2006) at a given population density of animals. More specifically, high roe deer abundance led to increased browsing damage on beech and other deciduous trees across the land use categories. However, as in pine forests, the relative browsing damage on beech and other deciduous trees was higher than for pine trees, suggesting that pine saplings were not preferred due to energetic or flavourful constrains. Because roe deer is a concentrate selector (Tixier et al. 1997), we suggest that under low roe deer densities deciduous trees other than beech are even preferred and beech is avoided due to different energy content. The concentration of soluble sugars was reported to be related to the avoidance of roe deer towards beech and preference to other deciduous trees such as hornbeam (Tixier et al. 1997). But with high animal densities, roe deer is forced to feed on beech, because selective browsing on other deciduous tree saplings is no longer sufficient. We suggest that negative effects of browsing damage may be most pronounced in mature deciduous forests, because of the absence of shrubs and herbs as alternative food. Additionally, natural occurring tree seedlings are rare in

mature deciduous forests due to suboptimal light conditions under closed tree canopy, leading to a massive decline in tree regeneration if browsing is high. Roe deer feeds more on species having either a lower amount of fibre, or increased contents of soluble sugars. On a large temporal scale, roe deer may change the diversity of deciduous trees by selectively feeding on species with high quality food contents such as oak, alder, and elm (Kullberg and Bergstrom 2001). It was even reported that under present-day grazing pressure pine and beech will become the dominant canopy species in the near future, because browse-sensitive tree species may not successfully regenerate (Kuiters and Slim 2002).

*Conclusion*

Relative animal abundance of deer species was disproportionately high in mature pine stands, whereas browsing damage was exclusively higher on deciduous trees than on pine trees. In the future, this preference may hinder for natural regeneration of deciduous trees in mature pine forests. The aimed transformation of mature pine forests to more natural beech or mixed deciduous forests may be very difficult under the given animal densities of deer in the study area. Lower deer densities in deciduous forests even resulted in enhanced browsing damage on deciduous trees due to lacked ground vegetation, whereas beech was less browsed. When mature pine stands will get rarer after forest transformation, ungulates will have to use habitats represented by beech and mixed deciduous forests even more frequently. Hence, we suppose that browsing damage in deciduous forests after forest transformation will increase under present day ungulate abundance. Due to a high browsing pressure on deciduous trees and the avoidance of beech, especially roe deer density will have to be reduced if natural regeneration of deciduous trees is desired. A low roe deer density is the base not only for structural rebuilding of mature pine forests, but is also crucial for persistent regeneration of deciduous trees and a high diversity of tree species. Finally animal numbers should be adjusted depending on the proportion and quality of winter food supply in certain habitats. Under the mean given winter food supply on our study plots, a mean of five ungulate units per100 ha (1 ungulate unit = 4 roe deer, or 2 fallow deer, or 1 red deer (Hofmann et al. 2009)) would be sustainable. After the hunting period in March 2009 we counted a mean of seven ungulate units per100 ha. In the future, forest managers and hunters will have to face the challenge to adjust deer density to a sustainable level to permit forest regeneration on a large spatial and temporal scale.

## General Discussion

In this study, I used the Biodiversity Exploratories to investigate the relationship between different types of land use in forest and grassland ecosystems and selected species of small and large mammals. I addressed the following question: ***Do increased or decreased land use have positive or negative effects on the diversity, abundance, and habitat use of selected mammal species.***

Additionally, I combined mammal monitoring data with different botanical and forestry survey datasets to further quantify the underlying mechanisms of land use affecting habitat attributes, and, thus, the mammal community.

### Study setup and target species

Land use change is a continuous process, which makes it difficult to investigate its effects on a single study site within a short period of time. However, many study plots with different land use types located in the same region would provide a suitable setup for simultaneous investigations and would represent a novel approach in biodiversity research. In Germany, the Biodiversity Exploratories form a large scale and long term research platform which allows for such concurrent observations of various taxa on identical study sites. Each Exploratory contains 300 experimental plots and incorporates the most common habitat types of that region. Hence, a broad spectrum of different land use types is available for the analyses of biodiversity change. All study plots were selected on the base of a large soil inventory in order to minimize site-specific differences in soil conditions. Different types of land use and management ranged from near natural and unmanaged sites to highly managed habitats in forest and grassland. The setup of the Biodiversity Exploratories combined with the used monitoring methods represents a "natural experiment" in which the response of selected mammalian species to changing land use was investigated on the species as well as on the individual level. Each Exploratory represents a study-replicate of this experiment, as the composition of land use types of the Exploratories is comparable. To my knowledge, this is the first attempt of a repeated "natural experiment" of this kind on a large scale in Germany using selected mammalian species.

In the present research, I have investigated the effect of land use on the occurrence and behaviour of small and large mammals. Both groups of mammals play a crucial role in the ecosystems they live in. Small mammals affect the ecosystem from the base (bottom up). Most importantly, they serve as a food resource for predators (Hörnfeldt et al. 1990, Korpimäki and Krebs 1996) and act as seed and spore dispersers (Maser et al. 1978). Therefore, a change in the small mammal community may affect the stability of food webs and alter the distribution of plants and fungi. In contrast, large mammals affect the ecosystem from the top (top down). For

instance, large herbivores have particularly negative effects on the ecosystem by browsing, grazing (Gill 1992a), and thereby reducing plant growth and survival (Gill 1992b). I showed that bottom up and top down processes are affected differently by changing land use. Thus, it was demonstrated that the investigation of both groups of mammals provides a more precise and complete picture of how land use can affect an ecosystem. My research further benefited from the interdisciplinary setup of the Biodiversity Exploratories through better understandings of these processes. Working groups who investigated diverse taxa across different trophic levels on a large scale provided a valuable opportunity to combine different datasets and test for interactions. Specifically, I benefited from botanical data and data on browsing damage collected during the forest inventories.

## The effect of different land use on small mammals

*The importance of habitat structure for small mammal species*

Increased habitat structure is characterized by more cover, high food resources, and decreased predation risk (Simonetti 1989, Moser et al. 2002), and can be increased by forest thinning that promotes spatial heterogeneity and diversity in plant communities (Carey and Wilson 2001). Previous studies have demonstrated that species richness and abundance of small mammals in forest habitats are positively influenced by shrub cover, understory vegetation, and structural heterogeneity (Ecke et al. 2002). Along these lines, managed forest stands have been found to yield higher numbers of small mammals (Suzuki and Hayes 2003). The results of the present study support the hypothesis, that management, at least on forest sites, favors small mammal species richness, abundance, and habitat use due to increased habitat structure and structural heterogeneity. Species richness and small mammal abundance was significantly higher on managed than on unmanaged forest plots. Analyses of botanical parameters indicate that higher species richness and abundance was mainly associated with higher structural heterogeneity, and in particular, with high shrub cover on the study plots. Species number and abundance was directly correlated with shrub cover in Schorfheide-Chorin and in the Schwäbische Alb. However, in Hainich-Dün, only lower tree cover had a positive effect on the distribution of small mammals on managed forest sites.

The small mammal species most frequently trapped on forest plots was *Myodes glareolus*, and its abundance was strongly correlated with high habitat structure, such as high shrub cover, which is in line with other findings highlighting the importance of shrub cover and structural heterogeneity (Ecke et al. 2002). In addition to shrub cover, *M. glareolus* was reported to be linked to habitats with developed undergrowth and fallen logs and branches, and used these structures as burrows (Miklos and Ziak 2002). The results of our study in Hainich-Dün support

this finding. Conversely, the abundance of *Apodemus flavicollis* was not as strongly related to habitat structure as it was found in association with *M. glareolus*. It has been reported that forest management resulting in age class forests of different tree species had a minor influence on the distribution and abundance of *A. flavicollis* (Marsh et al. 2001), although it has been proposed that *A. flavicollis* occasionally prefers high coverage of shrubs (Miklos and Ziak 2002). Contrarywise, *A. flavicollis* was also found to be more abundant in mature forests (Stenseth et al. 2002), but the present study found no support for this.

The trapping data in grassland habitats do not support the hypothesis of increased small mammal species richness and abundance with high management intensity. More specifically, unmanaged but structural complex study sites with high grass cover yielded the highest species richness and trapping numbers. This lends supports to the notion that among grasslands high management intensity caused by frequent mowing and grazing decreases small mammal species richness and abundance, and can act as a major threat if performed over large areas (Evans et al. 2006). Therefore, this coincides with the idea that shelter belts, woodlots, and a high spatial heterogeneity may conserve small mammal diversity in highly managed areas (Bignal and McCracken 1996). My data imply that different animal numbers in grassland between the Exploratories were most likely due to variances in soil depths and soil structure, and thus, different potential for burrowing for subterraneously living voles. Optimal soil conditions, i.e. thickness and looseness, in Schorfheide-Chorin may have caused the high trapping numbers, especially of *Microtus arvalis*.

Results of the radio tracking study in Hainich-Dün indicate that structural heterogeneity was extremely important for *M. glareolus* and *A. flavicollis*. Both species strongly preferred deadwood rather than tall vegetation on forest plots, but *M. glareolus* showed stronger avoidance towards large herbs compared to *A. flavicollis. A. flavicollis* is known to better escape a predator (Görner and Hackethal 1988) when located in areas with tall vegetation. My findings indicate that deadwood, such as stumps and big log clusters, provided a better hiding opportunity than tall vegetation on account of being a stronger physical obstacle for predators. Thus, predator avoidance may be one of the driving forces in small mammal behaviour, determining the individual usage of habitat structures in forests.

This study demonstrates that the distribution of small mammal species and animal abundance is affected by the cover of shrubs and trees, deadwood, as well as the diversity of herbs. It has been previously reported that understory vegetation combined with coarse woody debris can account for the variation of small mammal species in managed forest stands (Mengak and Guynn 2003). Deadwood and understory vegetation can provide favorable microhabitats for

several small mammal species (Carey and Johnson 1995). Accordingly, it is highly recommended that the preservation of such microhabitat characteristics should be increased for the purpose of biodiversity conservation (Carey and Johnson 1995).

*Methodological remarks*

Live trapping was used to monitor small mammals in the Biodiversity Exploratories because this method creates a robust measure of relative animal abundance if a sufficient number of trapping nights are used. Per study plot and year, I used 15 trapping nights (five live traps for three consecutive nights), the maximum number that could be implemented in the setup of the Exploratories. Because low recapture rates did not allow for other mark-recapture indices, I used the number of first captures as an estimate of relative animal abundance. The use of "Ugglan" multiple live capture traps allowed for trapping a broad spectrum of small mammal species, ranging from shrews up to edible dormice. Live trapping with this type of trap is favourable for cost effective and meaningful monitoring, by creating data on species richness and relative animal abundance. However, live trapping only reveals changes in trapping numbers depending on habitat attributes, and is not efficient for describing the detailed habitat use of a species. Therefore, data on microhabitat use of small mammals derived from trapping results should be interpreted with caution (Yahner 1982). Moreover, data derived by live trapping can often be biased due to external food availability reducing bait acceptance and trapability (Fitch 1954). Thus, reduced trapping numbers in Schorfheide-Chorin and Hainich-Dün in 2009 may result from increased tree seed production (unpublished data).

Radio tracking, alternatively, had provided fine scaled data on the microhabitat use of the two small mammal species most frequently trapped in the forest. Location data did not reflect the trapability, but represented the actual occurrence of animals during a longer period of time than during the three single trapping nights. Combined with the entire mapping of the study area, microhabitat use could be analyzed in detail and revealed more fine scaled information than any other data derived by live trapping. However, the method of radio tracking is labour and cost intensive, and was therefore only conducted on six study plots in the Hainich-Dün Exploratory. The results derived by radio tracking depend highly on sample size, the selection of study plots, as well as on radio tagged individuals (Kenward 2001). Therefore, it is recommended that the number of study plots and radio tagged animals should be increased in future studies to reduce the confounding variance on microhabitat use. Ultimately, the combination of live trapping and radio tracking on all 300 experimental plots of the Exploratories would have been the ideal means of investigating species richness, relative abundance, and microhabitat use of small mammals in relation to land use change.

## The effect of different land use on large mammals

*The importance of food availability for large mammal species*

Spotlight counting was one method applied to monitor large mammals in the Biodiversity Exploratories. Data on harvest rates and spotlight counting indices of observed species were positively related, yet, on average, more animals were counted than shot. This, however, may be accounted for by the harvesting management strategy because only the annual rate of population increment is culled to maintain a relatively stable population density. My results therefore support the view that spotlight counting is a robust method to reveal differences in population trends (McCullough 1982, Acevedo et al. 2008). Of additional importance, the habitat use of roe deer and fallow deer largely differed between the Exploratories, which was attributed to be caused by the different quantities of winter food supply (Hofmann et al. 2009) between habitats in the three regions. Specifically, spotlight counting data revealed patterns of habitat segregation between roe deer and fallow deer, where both species occurred. Pine forests in Schorfheide-Chorin contained high amounts of usable food plants (e.g. wintergreen herbs), and were more intensely used by fallow deer. In contrast, deciduous forest stands in Schorfheide-Chorin contained little quantities of winter food, and were avoided by fallow deer; roe deer, however, was attracted to this kind of habitat (Focardi et al. 2002). These results imply that fallow deer prefer habitats with high winter food supply, and forces roe deer to use suboptimal habitats such as deciduous forests (Focardi et al. 2006). It has been previously shown that species-specific grazing can modify the habitat structure in favour of one species (Focardi and Tinelli 2005). More importantly, roe deer has been found to be more affected by dietary competition (Latham et al. 1999). It follows then that in the present study the deciduous forests were avoided by fallow deer most likely because of suboptimal food availability.

Faecal pellet group counting was only conducted in Schorfheide-Chorin. Roe deer and fallow deer showed a clear preference for mature pine stands relative to all other forest types. Additionally, both species showed strong avoidance towards unmanaged beech forests, providing neither food resources nor shelter. Previous work on roe deer behaviour reported a strong relationship with high food availability and understory cover (Tufto et al. 1996). Thus, the deer's preference for mature pine forests may be explained by their dependence on a high quality winter food supply, which was more pronounced in regions with decreased large tree cover. Roe deer were more abundant in deciduous forests than fallow deer, suggesting that this species is able to shift from ground vegetation to other food resources, such as saplings of deciduous trees (Görner and Hackethal 1988). Fallow deer showed a preference for mature pine forests and a stronger avoidance towards deciduous forests than roe deer, which corresponds

with the result of the spotlight counting surveys. Additionally, fallow deer abundance was inversely related to the degree of canopy cover, which results from increased growth of feeding plants due to increased light availability (von Oheimb and Härdtle 2009). Mature pine forests yielded the highest estimates of deer abundance. Although they are not intensively managed (pers. comm.), they represent an optimal habitat for deer in terms of food availability during the winter. Low canopy cover in mature pine stands enhance the cover of small shrubs and herbs on the forest floor (pers. comm.), and therefore the quantity/quality of winter food supply. Although the reduced canopy cover in Schorfheide-Chorin led to increased animal abundances caused by high food availability, it may not necessarily be connected to high management intensity as such. The stand type and tree species were found to be by far more important in explaining large ungulate presence, e.g. mature pine stands yielded the highest animal numbers. Hence, based on the present data, I find no support for the hypothesis that land use concerning intensive management in forests favours large mammal diversity and abundance. However, the results of this study provide further support for the finding that unmanaged and mature deciduous forest sites represent a suboptimal habitat type for large ungulates.

The addition of data on browsing damage to the analysis of pellet counts allowed for more detailed information to be acquired on the relationship between large ungulate abundance and the effect on the tree vegetation. The results indicate that damage on pine trees was not strongly related to roe deer abundance. Therefore, the high amount of ground vegetation may have protected young pine trees from increased browsing damage as it was reported in other studies (Welch et al. 1991, deJong et al. 1995). In contrast, young deciduous trees suffered high specific browsing damage, although they are not very abundant in pine forests. The preference for young deciduous trees in pine forests can be explained by higher energy content and taste preference of deer (Tixier et al. 1997). On the other hand, deciduous forests contain few ground vegetation, which, in turn enhances deer browsing on tree saplings (Moser et al. 2006). Under low roe deer densities roe deer prefer deciduous trees but avoid beech (Kullberg and Bergstrom 2001) because it is a concentrate selector (Tixier et al. 1997). However, if the abundance of roe deer is high, browsing damage on deciduous trees, including beech, increases. Therefore, the negative effects of browsing damage may be most pronounced in mature deciduous forests, because of the absence of shrubs and herbs as alternative food. On a large temporal scale, roe deer may therefore affect the diversity of deciduous trees by selective feeding (Kuiters and Slim 2002).

*Methodological remarks*

In this study, spotlight counting has been demonstrated to be a valid method for monitoring large mammal species. However, more precise density estimates would be possible when

distance measurements of the counting area around the survey tracks and to the sighted animals would be recorded more accurately (e.g. laser range finder) as this can increase the precision of applied models (Focardi et al. 2002). Additionally, brushy vegetation may have reduced visibility along parts of the survey tracks to a minimum level so that data were not reliable as such. Patterns of deer habitat use collected from spotlight counting data should be interpreted with care whenever data has been collected over a short period of time (McCullough 1982). In the present research, this may have led to biased data which did not fully represent the true habitat use of the observed species. Spotting animals in a specific habitat type over a short period of time (i.e. three nights) does not necessarily provide information about the general habitat use of this species.

Faecal pellet group counting is a more accurate monitoring method in terms of habitat use, because data are gathered over a longer period of time, which is irrespective of weather or sighting conditions. However, this method is relatively labour intensive, since study plots must be visited twice, once for clearing old pellets before counting and then for data collection. Additionally, specific time constraints must be taken into account: counting has to be conducted immediately after snowmelt and before temperatures rise in order to avoid the decay of deposited pellets. Faecal pellet group counts resulted in higher estimates of animal abundance. In a comparative survey using spotlight counting, average animal sighting density was found to be 16% lower than estimates form faecal pellet group counts in the same area. However, observed pellet numbers may be disproportionally high on a local scale due to the attractiveness of mammals to the habitat. A reliable estimate of ungulate abundance can only be made by calculating the average animal density of a sufficient number of survey plots on a large area of several thousand hectares (Tottewitz et al. 1996). In terms of habitat use, I concluded that the results derived from the cumulative method of faecal pellet group counting are more reliable than those from spotlight counting. This is because data are collected over several weeks or months and are less error-prone, e.g. distance measurements. Therefore, the faecal pellet group counting method should be favoured whenever detailed information on habitat use of large ungulates is needed.

## Further implications and ecological consequences

This study demonstrates that changes in land use and management strategies affect small and large mammal species differently. Both species groups were associated with a specific type and degree of land use. In small mammals, species richness and animal abundance was higher in managed study sites than in unmanaged ones in the forest. In contrast, small mammals avoided sites of increased management and habitat disturbance caused by mowing or livestock grazing in

grassland habitats. However, there were no trappings of small mammals on fully unmanaged sites or near natural grassland sites in all of the Exploratories. In the case of large mammals, large ungulates strongly preferred mature pine stands but were not affected by high management intensity in the forests.

*The effect of forest canopy cover on small and large mammals*

The findings of this study indicate that in forest habitats, reduced canopy cover is the main parameter increasing species richness and abundance, as well as determining habitat use of small and large mammals. Forest management most often includes harvesting of trees, which reduces the degree of cover in the canopy layer. Such a reduction in canopy cover not only increases the structural heterogeneity in the upper forest stand (Carey and Wilson 2001), but also changes the light regime beneath the canopy layer down to the forest floor. As a result, plant growth and the overall structural heterogeneity in the forest stand increases (von Oheimb and Härdtle 2009). Although changes in forest canopy cover affected small and large mammal distribution, both groups reacted to different habitat attributes generated by canopy cover change.

The results of the present study demonstrate that small mammals rely on habitat structures, such as deadwood and dense vegetation (e.g. shrubs) for cover and shelter. Therefore, I propose that the small mammal abundance is highly affected by forest management, because as the number of harvested trees from the forest stand increased, the more plants will grow on the forest floor. The maximum management intensity of clear cutting further promoted small mammal abundance in this study, as very dense vegetation of young trees in reforested stands represented optimal conditions in terms of cover and shelter (Kirkland 1990, Moser et al. 2002). While forest floor structure had the largest effect on small mammal distribution, the stand type was relatively unimportant in determining small mammal abundance. For example, deciduous and coniferous forest stands had similar numbers of small mammals, as long as moderate management intensity guaranteed structural heterogeneity near the forest floor.

Compared to small mammals, large mammals showed a weaker response to increased forest floor structure and cover. Differences between species were supposedly driven by species-specific traits, including thermoregulation (Mysterud and Ostbye 1995, 1999). I propose that forest structure has little importance for cover and shelter against predators, since large ungulates in Germany have not suffered from large carnivore predation for several hundred years. More importantly, I suppose that large mammals, especially large ungulates, were influenced by the amount and distribution of food, particularly during winter. And again, food availability is additionally positively affected by reduced canopy cover through increased forest

floor plant growth. Therefore, forest management should have positive effects on large ungulate abundance by promoting forest floor plant growth (Smith et al. 2008). However, my data revealed that increased ungulate abundance and habitat use in mature pine forests in Schorfheide-Chorin did not necessarily result from increased management intensity. In addition to management, the stand type had a significant effect on animal distribution, as coniferous forests were more preferred than deciduous ones. Although not directly linked to forest management, coniferous forests have lower canopy cover than deciduous forests, which, in turn enhanced vegetation growth on the forest floor, and thus animal presence. Mature pine stands represent a common forest type in this area, which has not been intensively managed for up to one hundred years (pers. comm.). Here, young and recently managed pine stands had lower animal abundances and were less used by ungulates than were mature pine stands.

*The role of mature deciduous forests and ecological consequences of forest transformation*

Small and large mammal species reacted differently to forest management and stand type. However, both species groups had the lowest species richness, animal abundance, and habitat use in unmanaged or selection forests of deciduous trees. Accordingly, I propose that deciduous forests with low management intensity represent a suboptimal habitat for small and large mammals. Because mature and unmanaged deciduous forest stands have a closed canopy layer and low forest floor plant growth (Boch, unpublished data), they offer neither cover and shelter, nor sufficient food resources. Modern silvicultural practise and ecological forest management intend to transform monocultures of coniferous trees into beech or mixed deciduous forests with low management intensity in the near future (MLUR 2004). The results of this study imply that this transformation of forest stands will have negative effects on mammal communities. If most of the forest areas in Germany will incorporate mature and closed canopy deciduous stands, I assume that small mammal abundance will decrease due to low ground cover and increased predation pressure by mammalian and avian predators (Hörnfeldt et al. 1990, Korpimäki and Krebs 1996). As an ecological consequence, it may be supposed that low small mammal abundance and diversity would lead to decreased dispersal of tree seeds and spores of mycorrhizal fungi (Maser et al. 1978), and thus to a decline in natural tree regeneration and growth. Furthermore, predator species will suffer from reduced food availability, if small mammal abundance is decreasing (Korpimäki et al. 1991). This, in turn, would lead to population declines in the predator species themselves.

In contrast to the effect on small mammals large, ungulates will not likely undergo a population decline in mature deciduous forests, as they will not suffer from an increase in predation. Nevertheless, if mature deciduous forests will become more prevalent, it may be

expected that large ungulates will have to shift to food resources other than ground vegetation. As an ecological consequence, and under present day ungulate abundance, browsing damage and feeding on saplings of young deciduous trees will increase, impeding natural tree regeneration. If browsing damage on deciduous trees is high, tree and shrub growth will be reduced (Gill 1992b), disfavouring the structural complexity near the forest floor. Therefore, I anticipate that increasing browsing damage by ungulates may even disfavour small mammal presence in deciduous forests due to reduced structural heterogeneity. Roe deer density, in particular, would have to be reduced if natural regeneration of deciduous trees is to take place, because of this species' high browsing pressure on deciduous trees and the avoidance of beech (Kullberg and Bergstrom 2001). More specifically, I propose that present day ungulate abundance and the negative effects of browsing may have potential to complicate forest transformation from the beginning. To transform coniferous monocultures into beech or mixed deciduous forests, high rates of natural tree regeneration of deciduous trees are necessary. However, as demonstrated here, the tree-specific browsing damage on deciduous trees was much higher in pine stands than in deciduous forests. Hence, it could be difficult to transform coniferous forests into deciduous forests if the natural regeneration of deciduous trees is impeded by high deer browsing. I propose that low population density, especially of roe deer, is crucial for structural rebuilding of mature coniferous forests, for persistent regeneration of deciduous trees and a high diversity of tree species.

In the near future, the majority of Central European forest sites will undergo forest management on account of economic interests and the need for renewable resources. In the light of high diversity and abundance of small and large mammals, mature beech or mixed deciduous forests do not represent optimal habitats, but may incorporate the basic habitat requirements of these species groups in the case that a specific level of habitat structure is provided. As proposed in the ecological forest management practice, selection cutting forests should be implemented by harvesting single trees and avoiding clear cutting. This would lead to spots of increased light availability and increased growth of ground vegetation, and would allow for a higher structural complexity on managed patches. Additionally, deadwood and coarse woody debris should be left on site , as much as possible after management events in order to provide high structural components on the forest floor (Carey and Johnson 1995). Natural tree regeneration of beech and especially of other deciduous trees such as oak, elm, ash, maple or alder should be supported and trees should be replanted if necessary. Most importantly, large ungulate abundance, and roe deer abundance in particular, need to be reduced to an appropriate level, to allow for and to maintain the natural regeneration of a broad spectrum of tree species in

coniferous and deciduous forests. I propose that an adjusted ungulate abundance, and thereby induced tree regeneration, is essential to ensure both stable resource availability for forest management and a structural complexity in forest habitats that promote mammalian species richness.

## Summary

Landscapes have been changing due to human activity, resulting in forest fragmentation and spreading agricultural use. Intensification of land use resulted in increased landscape homogenisation characterised by monocultures and an overall loss of biocomplexity. The loss of biodiversity due to increased land use is supposed to have effects on ecosystem processes and services, and may thereby be connected to the wellbeing of humanity as a whole. Nowadays land use strategies in Central Europe are changing. The process of ecological forest management aims to transform forest monocultures into near natural deciduous forests with moderate or no management at all. At the same time financial support is given to ecological management procedures in grassland habitats. However, it is yet not fully understood if and to what extend these changes in management intensity will affect the communities in according habitats. Hence, research needs to be done to simultaneously investigate the complex interactions between different species groups and a variety of management strategies in forest and grassland habitats over a large spatial and temporal scale.

The Biodiversity Exploratories consist of three research sites Schorfheide-Chorin, Hainich-Dün, and Schwäbische Alb. Each site contains 100 study plots of different management types and land use classes ranging from near natural to intensively managed ecosystems. In the present study I used small and large mammals as target species, because they play a major role in forest and grassland ecosystems acting as food resource for predators, seed dispersers, as well as browsers or grazers. Thereby, I investigated the effect of changing land use in forest and grassland on small and large mammal species. Small mammals were live trapped over two years in all three Exploratories, yielding 1882 total captures during 7650 trapping nights. In combination with botanical data I investigated the link between habitat attributes and small mammal distribution. Additionally, 45 individuals of small mammals were radio tracked on six study plots in Hainich-Dün to investigate fine scaled habitat use. Furthermore, I conducted large mammal monitoring by using spotlight counting in all three Exploratories where 110 hours of nightly counting yielded 339 sightings of animals in forest and open land habitats. Thereby I estimated animal abundance and computed habitat use of selected species. Faecal pellet group counts of large ungulates were applied in the Exploratory Schorfheide-Chorin. Within two counting events 1036 pellet groups were counted and determined. I estimated animal abundance and computed habitat use of selected species. Furthermore, I was able to compare data on browsing damage with abundance estimates and habitat use of selected ungulate species.

During small mammal live trapping I found higher species richness and animal abundance on managed than on unmanaged forest plots rising with increased structural heterogeneity

mainly caused by high shrub cover. Radio tracking revealed that structural heterogeneity was also very important for the two most abundant small mammal species in the forest, whereas both species strongly preferred deadwood rather than large vegetation on forest plots in Hainich-Dün. Hence, understory vegetation and coarse woody debris are very important for small mammal species in managed forest stands, because of providing cover and shelter, and should therefore be increased for conservation purpose. In grassland, high management intensity caused by frequent mowing and livestock decreased small mammal species richness and abundance, and can act as a major threat if performed over large areas.

Large mammal monitoring using spotlight counting turned out to be a robust method to reveal differences in population trends. Habitat use of abundant roe deer and fallow deer largely differed between the Exploratories and revealed patterns of habitat segregation between these species. I suggest that fallow deer in this study showed a stronger potential to use habitats with high winter food supply. Thereby, roe deer was repelled to suboptimal habitats like deciduous forests, because this species was supposed to be more affected by dietary competition. Faecal pellet group counts revealed that roe deer and fallow deer clearly preferred mature pine stands, and both species showed strong avoidance towards unmanaged beech forests, providing neither food resources nor shelter. I explain the preference towards mature pine forests to be due to the dependence on high quality winter food supply. Data on browsing damage revealed that damage on pine was not related to high deer abundance, which I suggest to be due to alternative food represented by ground vegetation in pine forests. Damage on deciduous trees was exclusively higher, whereas beech was less browsed. I suggest, that negative effects of browsing damage are most pronounced in mature deciduous forests, because of no alternative food availability.

In this study small and large mammal species seemed to be affected by changes in canopy cover, which is a result of forest management and alters the light regime and structural heterogeneity on the forest floor. However, small mammals are directly determined by habitat structure and the need for cover and shelter, whereas large mammals depend on food availability affected by ground plant growth. Therefore, unmanaged or continuous cover deciduous forests represent suboptimal habitats for small and large mammal species. In the future, forest management procedures should create high levels of habitat structure, if high small and large mammal diversity is desired. Nevertheless, ungulate abundances should be adjusted to enable and preserve natural regeneration of a broad spectrum of tree species in coniferous and deciduous forests.

## Zusammenfassung

Der Mensch verändert seit seinem Auftreten die Landschaften der Erde mit dem Ergebnis von großflächiger Waldzerschneidung und der Ausbreitung landwirtschaftlich genutzter Flächen. Im Zuge der Nutzungsintensivierung entwickelten sich zunehmend Monokulturen, was mit einer Abnahme der Bio-Komplexität einherging. Dem durch erhöhte Landnutzung bedingten Rückgang der Biodiversität wurde in der Vergangenheit vermehrt das Potential zugesprochen, Ökosystemprozesse und ökosystemare Dienstleistungen negativ zu beeinflussen. Aktuell ändern sich Landnutzungsstrategien, wobei im Forst und auf Grünlandflächen eine ökologische Bewirtschaftung erreicht werden soll. Der ökologische Waldbau strebt z.B. die Umformung von naturfernen Nadelholzmonokulturen in naturnahe Buchen- oder Laubholzmischbestände an. Es ist jedoch nicht vollkommen geklärt, ob und in welchem Maße sich aktuelle Bewirtschaftungsänderungen auf die Organismengruppen in den entsprechenden Lebensräumen auswirken. Daher ist die Erforschung der Effekte von ändernder Landnutzung auf verschiedene Arten in großen räumlichen und zeitlichen Skalen von zentraler Bedeutung.

Die Biodiversitäts Exploratorien beinhalten drei Untersuchungsgebiete: Schorfheide-Chorin, Hainich-Dün und Schwäbische Alb, wobei pro Gebiet 100 Untersuchungsflächen unterschiedlicher Landnutzung von natürlichen bis intensiv genutzten Habitaten existieren. In der vorliegenden Arbeit untersuchte ich Klein- und Großsäuger, da diese Artengruppen wichtige Rollen als Beute, Samenverbreiter, aber auch als Äser in Wäldern und Grünländern übernehmen. Dadurch sollte der Effekt von unterschiedlicher Landnutzung auf Klein- und Großsäuger in Wald- und Grünlandhabitaten untersucht werden. Während Lebendfängen von Kleinsäugern in zwei Jahren wurden 1882 Fänge in 7650 Fangnächten verzeichnet. Nach Verschneidung mit botanischen Daten, konnte das Kleinsäugervorkommen in Abhängigkeit von Habitateingeschaften beziffert werden. Zusätzlich wurden 45 Kleinsäuger auf sechs Untersuchungsflächen im Hainich-Dün radiotelemtriert. Großsäuger wurden einmal mit Hilfe von Scheinwerferzählungen untersucht, wobei in allen Exploratorien 339 Sichtungen während 110 Zählstunden erreicht wurden und die Tierdichte und Habitatnutzung geschätzt wurde. Im Exploratorium Schorfheide-Chorin wurden mit Hilfe der Losungszählmethode 1036 Losungshaufen von Großsäugern aufgenommen und bestimmt. Auch hier wurden Tierdichte und Habitatnutzung geschätzt und zusätzlich mit Daten von Verbissschäden an Bäumen verschnitten.

Nach Auswertung der Kleinsäuger Lebendfangdaten ergab sich ein höherer Artenreichtum und höhere Tierdichte auf genutzten gegenüber ungenutzten Waldflächen mit steigender Strukturvielfallt, besonders hervorgerufen durch dichte Strauchdeckung. Die Auswertung der

Radiotelemetriedaten im Hainich-Dün deutete ebenfalls auf die Wichtigkeit der Strukturvielfallt für die häufigsten Kleinsäugerarten im Wald hin, wobei Totholzbereiche gegenüber hoher Vegetation von beiden Arten bevorzugt wurden. Demzufolge sind bodennahe Vegetation und Totholz für Kleinsäuger in genutzten Wäldern durch Schutz vor Prädation von entscheidender Bedeutung und sollten in Zukunft gefördert werden. Im Grünland wirkte sich Landnutzung durch Mahd und Beweidung hingegen negativ auf Artenzahl und Tierdichte von Kleinsäugern aus und kann somit großflächig den Kleinsäugerbestand dezimieren.

Die Scheinwerferzählung für Großsäuger erwies sich als robuste Methode, um Populationsunterschiede aufzudecken. Dichte und Habitatnutzung von Reh und Damhirsch unterschieden sich und wiesen auf eine Habitat Trennung hin. Ich gehe davon aus, dass der Damhirsch ein stärkeres Potential zur Nutzung von Habitaten hoher Nahrungsverfügbarkeit besitzt. Da das Reh mehr von Nahrungskonkurrenz betroffen sein soll, kann diese Art somit in suboptimale Habitate wie Laubholzbestände mit niedriger Nahrungsverfügbarkeit verdrängt werden. Daten der Losungszählung ergaben, dass Reh und Damhirsch alte Kiefernforste bevorzugten, während ungenutzte Buchenforste mit niedriger Nahrungsverfügbarkeit gemieden wurden. Somit erschließt sich für mich die Nahrungsverfügbarkeit als Hauptursache für das Vorkommen von Reh und Damhirsch. Trotz hoher Tierdichten gab es keine erhöhten Verbissschäden an Kiefern, was durch die hohe Verfügbarkeit an Alternativäsung in Kiefernaltbeständen erklärbar ist. Der Verbissschaden an Laubbaumarten war ausschließlich höher, wobei die Buche weniger verbissen wurde. Durch geringe Alternativäsung wird deshalb der nachhaltige Schaden durch Baumverbiss in Laubholzbeständen sehr hoch sein.

Auf Grund der Datenlage scheinen Klein- und Großsäuger letztendlich von Änderungen der Baumkronenstruktur abhängig zu sein, die sich durch Waldnutzung ergeben und Auswirkungen auf die Lichtverfügbarkeit und Strukturvielfallt am Waldboden haben. Kleinsäuger sind allerdings auf die eigentliche Habitatstruktur und den Schutz vor Prädatoren angewiesen, wobei die Verteilung der untersuchten Großsäuger dem bodennahen Pflanzenwachstum und der entsprechenden Nahrungsverfügbarkeit unterliegt. Somit erscheinen ungenutzte oder alte Laubbaumbestände als ungeeignete Habitate für Klein- und Großsäuger. Zukünftige Nutzungsstrategien im Wald sollten sich um die Schaffung von maximaler Strukturvielfallt bemühen, um die Diversität von Klein- und Großsäugern zu fördern. Allerdings sollten die Dichten von großen Herbivoren z.B. des Rehs reduziert werden, um eine natürliche Verjüngung vieler Baumarten in Nadel- und Laubwäldern zu ermöglichen und langfristig zu sichern.

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## Acknowledgements

The work has been funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories". Field work permits were given by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).

I would like to thank Prof. Dr. Stefan Halle, Prof. Dr. Elisabeth Kalko, and Prof. Dr. Wolfgang Weisser for supervision, scientific support and revision of the manuscripts. I have to thank Dr. Robin N. M. Feeney, who revised the general introduction and discussion.

Special thanks go to the following people of the Biodiversity Exploratories who helped with preliminary work in the local management teams, logistic support during field work, permissions, or scientific support (alphabetical order): Martin Fellendorf, Maren Gleisberg, Sonja Gockel, Martin Gossner, Matthias Groß, Jörg Hailer, Andreas Hemp, Dominik Hessenmöller, Ingo Homrighausen, Kirsten Jung, Ralf Lauterbach, Norbert Leber, Ilka Mai, Jens Nieschulze, Simone Pfeiffer, Ulf Pommer, Swen Renner, Mandy Scholz, Ingo Schöning, Uta Schumacher, Claudia Seilwinder, Tim Walther, and Konstans Wells.

Special thanks go to all Hiwis and student helpers who enabled simultaneous field work in the Exploratories: Kerstin Andreas, Nadine Bandemer, Evelyn Böhm, Taina Conrad, Jan Esefeld, Konstantin Falck, Isabelle Flaig, Leila Gaigl, Franziska Hüther, Antje Jakupi, Alexander König, Antje Nöthlich, Sandra Rienow, Anja Rügauf, Jenny Schuster, and Karsten Swinnes.

Furthermore I would like to thank the following colleagues for supporting advises and pleasant atmospheres on the field sites during field work and several PhD and annual meetings: Michaela Bellach, Steffen Boch, Stefan Böhm, Erik Grüneberg, Valentin Klaus, Esther Kowalski, Markus Lange, Jörg Müller, Carolin Seele, Stephanie Socher, Manfred Türke, and Jana Wäldchen.

Finally, I have to thank my family for their help and support during the time of the work, and most of all Anne Friederike Kachel for being so much more than just a helping hand during the hard times of field work and writing. I will not have to point out your personal contribution to this work; you know that I would not have come this far without you!

**Manuscripts / Publications**

Heinze, E., S. Boch, M. Fischer, D. Hessenmöller, B. Klenk, J. Müller, D. Prati, E.D. Schulze, C. Seele, S. Socher & S. Halle (2010): Habitat use of large ungulates in northeastern Germany in relation to forest management. Forest Ecology and Management, 261, 288-296

Türke, M., Heinze E., Svendsen S.M. & W. Weisser (2010): Seed predation in ant-dispersed plants by molluscs and rodents and the potential for seed dispersal by slugs. Oecologia, 163, 681 - 689

De Villiers, M.S., S. Mecenero, E. Heinze, M. Leshoro, L. Merbold, A. Nordt, N.M. Parsons & H.-U. Peter (2010): Introduced European rabbits *Oryctolagus cuniculus* at Robben Island: Population trends and management recommendations. In prep. for South African Journal of Wildlife Management

**Congress contributions**

Heinze, E., Halle, S., (2007): Spatial behaviour of female common voles at low density. In: Abstractband 6th International Zoo and Wildlife Research Conference on Behaviour, Physiology and Genetics, IZW, Berlin: 102.

Heinze, E., Halle, S., (2008): Large mammal diversity in relation to landscape structure. In: Abstractband EURECO-GFOE 2008 annual meeting Band 38: 582

Heinze, E., Halle, S., (2010): Habitat use of large ungulates in North East Germany in relation to forest management. In: Abstractband, Mammalian Biology / Zeitschrift für Säugetierkunde, Special issue to volume 75: 11-12

**Grants**

Marie Curie funding for congress and training course "BIOSEB" (Summer school in Ecology and Biodiversity, Bialowieza, Poland (May 28th – June 2nd 2007).

Jena, Februar 2011 .....

Eric Heinze

## Selbständigkeitserklärung

Ich erkläre, dass ich die vorliegende Dissertation mit dem Titel DISTRIBUTION AND HABITAT USE OF SELECTED SMALL AND LARGE MAMMAL SPECIES IN RELATION TO DIFFERENT LAND USE selbständig und nur unter Verwendung der angegebenen Hilfsmittel und Literatur angefertigt habe.

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